CONTRIBUTIONS TO MAMMALOGY IN HONOR OF KARL F. KOOPMAN

THOMAS A. GRIFFITHS and DAVID KLINGENER, EDITORS

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Karl F. Koopman: A Biography and Bibliography

DAVID KLINGENER[1] AND THOMAS A. GRIFFITHS[2]

Karl Koopman was born on April 1, 1920, in Honolulu, Hawaii, the son and first child of Karl H. and Martha (Brown) Koopman. His sister, Elinor, was born two years later. As a child he lived in a number of places in and around the Los Angeles area, and he spent much time visiting the L.A. County Museum of Natural History, where he developed his lifelong interest in the natural history of birds, herps, and mammals. Karl attended high school in Red Hook, New York, his father being at the time a faculty member at Bard College. He enjoyed the science classes he took in high school and when it came time to attend college, Karl entered Columbia University intending to major in chemistry. Fortunately for the science of mammalogy, Karl enjoyed his zoology classes much more than his chemistry, and he switched majors in the middle college years, graduating in 1943 with a B.A. in zoology. He continued at Columbia as a graduate student, earning the M.A. in 1945 and the Ph.D. in 1950. As a graduate student he spent a great deal of time at the American Museum of Natural History. His fellow graduate students at the Museum included Ernest Williams, Max Hecht, Samuel McDowell, and Rodolfo Ruibal. Karl's interest in mammals, particularly in bats, and in systematics, distribution, and biogeography certainly was enhanced during this period.

Because work in those areas was then "unacceptable" in zoology at Columbia, Karl wrote his doctoral dissertation in the field of evolutionary genetics under the direction of Theodosius Dobzhansky. His thesis was on experimental strengthening of behavioral isolating mechanisms between laboratory populations of *Drosophila pseudoobscura* and *D. persimilis*. It tested the hypothesis that selection against hybrids would strengthen any incipient premating isolating mechanisms present in two sympatric populations. The paper resulting from this study was his first published work (1950) and is still frequently cited.

Karl spent a year teaching at the Middletown Collegiate Center (1949–50) and six years as an Instructor in Biology at Queens College. Tiring of teaching premeds the intricacies of the vertebrate body, he moved to the Academy of Natural Sciences of Philadelphia in 1958 as Assistant Curator of Mammals and then to the Field Museum of Natural History in Chicago as Assistant Curator of Mammals the next year (fig. 1). In 1961 he returned to the American Museum of Natural History in New York as Assistant Curator of Mammals, reaching the rank of Associate Curator in 1966 and Curator in 1978 (fig. 2). In 1985 he became Curator Emeritus at the American Museum and, freed of committee work and other distractions, devoted full time to his continuing study of bat systematics, evolution, and distribution.

Karl's fieldwork in the tropics began with a collecting trip to Jamaica in 1950. Between 1950 and 1970 he made numerous trips to localities in the Greater and Lesser Antilles, the Bahamas, the Virgin Islands, Mexico, Uruguay, and Bolivia. He also embarked on a series of trips to conferences, combined with working visits to museums in South America, England, various European countries, the U.S.S.R., Australia, and various African countries.

For the first fifteen years, Karl's publica-

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Fig. 1. Karl Koopman as an Assistant Curator at the Field Museum of Natural History. Photograph taken in the late 1950s.

Fig. 2. Karl Koopman as Curator at the American Museum of Natural History, mid-1980s.

tions were on the systematics, distribution, biogeography, and fossil history of the mammals and birds of the Antilles, the Bahamas, and Mexico. In 1965 he published a reanalysis of the bats from the American Museum Congo Expedition, the first of a continuing series of papers on the bats of Africa. His major synthetic work in this series was his 1975 monograph of the bats of the Sudan. Major analyses of the bat faunas of tropical Australia, New Guinea, and South America have also appeared.

Sound biogeography requires a sound basis in systematics. Karl's careful and comprehensive contributions to the purely systematic literature include the checklist of genera and species of bats in the 1982 *Mammal Species of the World* (edited by J. H. Honacki, K. E. Kinman, and J. W. Koeppl), the chapter on bats in the 1984 *Orders and Families of Recent Mammals of the World* (edited by S. Anderson and J. K. Jones, Jr.), the series of papers on the living families of bats in *Bat Research News,* and the forthcoming "Systematics of Chiroptera" chapter in the *Handbuch der Zoologie.* Karl is one of only two living chiroptologists (the other is J. E. Hill) who studies and understands systematics and distribution of bats of the world. He and Hill can be compared only with Dobson, Andersen, and Miller.

Karl has always been active in the American Society of Mammalogists, serving on the Board of Directors and as a member of the Nomenclature, Checklist, and Editorial committees. For his meritorious service to the Society, Karl was awarded the Hartley H. T. Jackson Award in June 1988. For his outstanding contributions to the science of mammalogy, Karl was made an Honorary Member of the American Society of Mammalogists in June 1990. He has been recognized in similar fashion by the smaller, more informally organized North American Bat Society. Since the second meeting in 1971, he has attended every one of the North American conferences on bat biology. In 1977 at the meeting in Ottawa, Canada, the members of the society paid him their highest tribute by awarding him the Gerrit S. Miller Award.

Late in 1988, David Klingener, Timothy J. McCarthy, and G. Ken Creighton discussed the idea of a *festschrift* volume for Karl as one more fitting way of honoring a person whose contributions to mammalogy have been profound. Their idea struck a responsive chord in others who had been entertaining similar thoughts since Karl's retirement in 1985. The idea, as finally proposed by T. A. Griffiths and D. Klingener to the administration at the American Museum, would be a volume of contributed papers dedicated not merely to Karl's deepest interest in chiroptology, but also to his multiple and varied interests in other areas of mammalogy. It was decided that the majority of the papers would be on chiropteran evolution, systematics, and zoogeography, but that other papers would be accepted as well. In particular, it was deemed appropriate that all full-time scientific staff in the Department of Mammalogy should contribute, regardless of the focus of their work.

Karl willingly shares his extensive experience and his understanding of the literature of mammalogy with others. Although he has not been involved with formal teaching for a number of years, Karl has served on the doctoral committees of such students as Patricia Freeman, Tom Griffiths, Sam McDowell, James Dale Smith, and Fred Szalay. He has mentored scores of other pre- and postdoctoral visitors to the American Museum, and has willingly given his time and expertise to colleagues the world over. He has no hesitancy in making his opinion known. One presents a paper at a scientific meeting with some trepidation, knowing that when one finishes, a hand will shoot up in the third row and a voice will say, "Weeeeell, it seems to ME that. . . ."

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The Identity of *Phyllostoma planirostre* Spix, 1823 (Chiroptera: Stenodermatinae)

CHARLES O. HANDLEY, JR.[1]

ABSTRACT

The description of *Phyllostoma planirostre* (Spix, 1823) was based on three specimens that Spix had collected near Bahia, Brazil. The name *Phyllostoma planirostre* has been used almost continuously since 1823, but it has been subject to various interpretations. Finally it was clearly defined by Andersen (1908), but a recently selected lectotype does not agree with Andersen's description.

Two of the original three cotypes still exist in the Munich Zoological Museum. Each has been designated lectotype of *Phyllostoma planirostre*. The two specimens represent different taxa, *Artibeus planirostris* Spix (= *A. jamaicensis planirostris*) and *A. fimbriatus* Gray. The two species are differentiated.

INTRODUCTION

During the years 1817–1820 Johann B. R. von Spix, accompanied by the botanist Carl von Martius, traveled widely in Brazil on behalf of the Museum of the Munich Academy of Science (Hershkovitz, 1987: 27). Among the more common bats of Brazil is a species described by Spix (1823) as *Phyllostoma planirostre*. Today Spix's bat is variously referred to as *Artibeus planirostris planirostris* and *Artibeus jamaicensis planirostris*. Handley (1987, 1990) used the latter combination. Compared with *Artibeus jamaicensis fallax* Peters—the common large, pale brown, 3/3 molar race of *A. jamaicensis* Leach in most of Brazil—*A. j. planirostris* Spix is considerably smaller. This is the conventional picture of *Phyllostoma planirostre* Spix. However, amazing as it may seem, after 166 years of continuous use, Spix's (1823) *Phyllostoma planirostre* has yet to be unequivocally identified, even though Spix's specimens are remarkably well preserved and have been subjected to an unusual amount of study and comment.

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I am grateful to the curators who kindly allowed me access to the collections of *Artibeus* in the following museums: American Museum of Natural History (AMNH), British Museum (Natural History) (BM), Museu de Zoologia Universidade de São Paulo (MZUSP), and Museum of Comparative Zoology (Harvard University) (MCZ). I have special thanks for Maria Rutzmoser (MCZ) and Paulo Vanzolini (MZUSP), who loaned me critical specimens for comparisons at the Smithsonian. The manuscript benefited from the advice and criticism of Darelyn Handley, A. L. Gardner, and T. A. Griffiths.

OBSERVATIONS

SPIX (1823)

Among the bats that Spix (1823: 66 and pl. 36, fig. 1) collected during his Brazilian expedition and later described was *Phyllostoma planirostre* from "suburbiis Bahiae" (= near Salvador, Bahia, Brazil). For *Phyl-*

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lostoma planirostre, Spix provided external measurements (among them, converted to millimeters from the old German zoll, head and body length 96 mm and forearm 62 mm); detailed descriptions of lips, noseleaf (lower edge of horseshoe free), and ears; mention of the wings; and even the color of the claws. Pelage of both upper and underparts, he wrote, was gray ("Corpus robustius, supra et infra canescenti-pilosum; alae nigrae . . ."). He did not mention stripes and the figure shows no facial stripes. Unquestionably Spix was describing a large *Artibeus.*

WAGNER (1840)

Wagner (1840) found in the Spix collection in Munich three specimens in alcohol that he supposed represented Spix's (1823) *P. planirostre.* Wagner synonymized *P. perspicillatum* Geoffroy, *P. planirostre* Spix, *P. obscurum* Schinz, and the "Grand fer-de-lance" of Buffon with *Vespertilio perspicillatus* Linnaeus, and he redescribed the species, based on Spix's specimens. Thus, from Wagner we have a more detailed description of *P. planirostre* than Spix provided. Wagner opened the mouth of one of the three specimens of *P. planirostre* and found that it had 4/5 postcanine teeth (= 2/3 molars). The horseshoe of the noseleaf was separated from the lip by a raised rim rather than a free edge ("eine Furche auch hier dasselbe von der Lippe abgrenzt"). Coloration was "dark gray-brown, somewhat paler below" ("dunkel graubraun, unten etwas lichter"). One of the specimens had facial stripes, which Wagner described as "lighter but poorly marked" ("zeigt sich ein lichter, aber wenig markirter Längsstreif"). Wagner's measurements of one of the Spix bats coincide closely with those given by Spix (1823). The only disagreement in the descriptions of Spix and Wagner concerns the lower edge of the horseshoe below the noseleaf—free or bound down.

WAGNER (1855)

Wagner (1855) again described *P. perspicillatum,* but in contrast to his 1840 description, which was based solely on Spix's specimens, by this time he must have had more specimens. He again used his 1840 measurements, but the rest of the description expressed more variation (e.g., dorsal coloration from sooty blackish-brown to rusty brown—"russig Schwarzbraunen ins Rostbraune"—and face usually striped—"vom Nasenblatt gewöhnlich beiderseits ein weisslicher Streif gegen das Ohr verlaufend." Thus, this description is not useful in the effort to recognize *P. planirostre* Spix.

PETERS (1865)

Peters (1865) borrowed the bats of Spix's collection from Munich and published a detailed account of their relationships. However, he dismissed *P. planirostre* with a single sentence: "Nach Untersuchung des einzigen Originalexemplars in Weingeist kann ich nur die Übereinstimmung desselben mit *Ph. perspicillatum* Geoffroy bestätigen. Gebiss 2.2/3.2 1/1 4/4 1/1 2.2/2.3."

Andersen (1908: 239) learned from W. Leisewitz of the Munich Zoological Museum of correspondence between Siebold of Munich and Peters regarding the loan to Peters of the bats of the Spix collection. This indicated that there actually were two specimens of *P. planirostre* in the Spix collection at that time, not just one as implied by Peters (1865).

ANDERSEN (1908)

Possibly there still were two or three specimens of *P. planirostre* in the Spix collection when Leisewitz corresponded with Andersen (1908).

FIRST SPECIMEN:

> The register of the Munich Museum . . . for 1830 has this entry: "No. 65, *Phyllostoma planirostrum* (Sp.), 1 Exemplar"; the specimen is labelled "Bahia, Spix coll."; this settles the question as to the number of typical specimens; there is one only [it was the custom of European zoologists of Spix's era to regard the first of several specimens in a list as the type]. . . . This [specimen] . . . has, Dr. Leisewitz writes, a distinct M3 on both sides of the upper jaw [evidently Leisewitz opened the mouth, for elsewhere he stated "the true type . . . shows no trace of having had the mouth opened for examination of the molars"]; the anterior margin of the horseshoe is (as said by Spix) free; the forearm measures 58.5, third metacarpal 57, first phalanx of third digit 17.7, second phalanx of third digit 28.5. This settles beyond all doubt, the identification of Spix's type. . . .

> As a final result: there is one type only of Spix's *Ph. planirostre,* still in the collection of the Munich Museum; this specimen has 3/3 molars, and the forearm 58.5 mm. . . .

With these words, this specimen, with 3/3 molars and a forearm of 58.5 mm, said to be no. 65 in the Munich Museum, became the lectotype of *Phyllostoma planirostre* Spix, selected by Andersen (1908).

SECOND SPECIMEN: The other specimen presumably is the one whose mouth was opened by Wagner, reported by Wagner (1840) and Peters (1865) to have 2/3 molars, regarded by them as representing *P. planirostris* Spix, and used, at least in part, by Wagner (1840) for his description of *P. perspicillatum.* According to Wagner (1840), the forearm of this specimen was 62 mm; according to Kraft (1982), 63.8 mm.

THIRD SPECIMEN: Whether the third specimen reported by Wagner (1840) was in the Munich Museum in 1906 is not clear. Only two specimens were specifically mentioned by Andersen (1908), but the following statement suggests that there were three: "When Wagner mentioned three typical examples, the reason was, I am informed by Dr. Leisewitz, probably that Spix brought back from Bahia not only one *Ph. planirostre* but also two '*Ph. perspicillatum*' . . . both of which latter are also in the Munich Museum. . . ."

CARTER AND DOLAN (1978)

When Dilford Carter visited Munich in 1966 he found only a skull and partial skeleton, which he presumed to be the type of *P. planirostre* Spix (Carter and Dolan, 1978: 64):

> ZSM 66: adult of undetermined sex; partial skeleton; Salvador, Bahia, Brazil; Spix; date of capture not specified. Holotype or syntype.
>
> *Skin.*—Not located and presumed lost.
>
> *Skull.*—Molars 2/3 [measurements made by Carter p. 120].
>
> *Remarks.*—ZSM 66 is a dry partial skeleton (skull, axial skeleton, pectoral girdle, and rib cage) probably that of a subadult inasmuch as the basioccipital and basisphenoid are not fused. The type locality is based on Spix' statement "habitat in suburbiis Bahiae" (now known as Salvador). A white label on the specimen bears the notation: "1903/9428 [=1903/9438] Bibia/ aus Alkohol (Skelett)/Spix. coll. Type."

KRAFT (1982)

Actually, two of Spix's specimens of *P. planirostre* still exist (Kraft, 1982, 1983). Spurred by the discovery in the Munich Zoological Museum of material of *P. planirostre* that Carter had missed ("At present, there are two original specimens of *Phyllostoma planirostris* at the ZSM, both complete with skin, skull, and skeleton"), Kraft (1982) figured the two skulls and described the coloration of the pelage of the two skins (which he supposed had been prepared from the alcoholic specimens between 1903 and 1927). The pelage of both specimens had faded to near Cinnamon Brown and neither had recognizable facial stripes.

Because of its larger size (forearm 63.8 mm, greatest length of skull 29.7 mm, maxillary, toothrow length 12.9 mm, and greatest length of mandible 21.5 mm) and assumed adulthood, Kraft (1982) designated no. 66 (1903/9438), the specimen with 2/3 molars, as lectotype of *P. planirostris* Spix. This must be the specimen whose dentition was examined by Wagner (1840) and the one with 2/3 molars that was disclaimed as the type of *P. planirostre* by Andersen (1908).

The smaller specimen (1903/9437) (3/3 molars, forearm 59.9 mm, greatest length of skull 27.8 mm, maxillary toothrow length 10.8 mm, and greatest length of mandible 19.1 mm), assumed by Kraft (1982) to be juvenile or subadult, was designated by him to be a paralectotype. This evidently is the no. 65 of Andersen (1908), which had 3/3 molars and a forearm of 58.5 mm.

Because Andersen (1908: 239) specified that no. 65 of the Spix collection, with 3/3 molars and forearm 58.5 mm, is the "type" (= lectotype) of *P. planirostre* Spix, Kraft (1982) could not choose another specimen as lectotype. Kraft's selection of no. 66 as lectotype and the labeling of this specimen as "type" by someone before Kraft are invalid. The lectotype of *P. planirostre* Spix by prior selection of Andersen (1908), the first revisor, is no. [65]/1903/9437, the smaller bat with 3/3 molars.

CONCLUSIONS

Despite the discrepancies, Kraft's (1982) paper is exceedingly valuable. With it and the

meager clues of earlier authors, together with the support of other collections of *Artibeus* from eastern Brazil, at last it is possible to identify *P. planirostre* Spix! Clearly, as suspected by Dobson (1878) and Andersen (1908), *P. planirostre* is a composite of at least two species.

The lectotype, no. [65]/1903/9437, is an adult specimen (not young as assumed by Kraft). It represents *Artibeus planirostris* in the sense of authors since Andersen (1908). *A. planirostris* is a junior synonym and geographic variant of *Artibeus jamaicensis* (Handley, 1990). The lectotype is characterized by small size (forearm 58.5 mm according to Andersen, 1908; forearm 59.9 mm, greatest length 27.8 mm, and maxillary toothrow length 10.8 mm according to Kraft, 1982); molars 3/3; coloration pale brown, a little paler below; facial stripes obsolete or absent; lower margin of horseshoe free; interfemoral membrane sparsely haired; rostrum short and arched.

No. 66/1903/9438 is a specimen of a juvenile, as observed by Carter and Dolan (1978) and clearly shown by Kraft's (1982) figure 1 (basicranial sutures not ossified). Based on Kraft (1982), this specimen is characterized by large size: forearm 63.8 mm (62 mm according to Wagner, 1840), greatest length of skull 29.7+ mm (probably longer, judging by figure 1, which shows the toothbearing portion of the premaxillae broken), maxillary toothrow length 11.3 mm (Carter and Dolan, 1978) or 12.9 mm (Kraft, 1982), molars 2/3; rostrum long, not greatly arched, and somewhat swollen laterally; and facial stripes obsolete or absent. Judging by figure 1, Carter probably measured the left toothrow, which appears normal as far as the canine–M2 length is concerned, although the anterior premolar is misaligned and displaced; while Kraft probably measured the right toothrow, which has the canine misaligned and displaced. Other characters referred to by Wagner (1840) may apply to this specimen: coloration dark gray-brown, paler below; horseshoe of noseleaf bound down and rimmed on lower edge.

Actually, the description and figure of no. 66/1903/9438 do not fit any species of *Artibeus* that has been reported to occur in eastern Brazil, but they agree in every detail with *A. fimbriatus* Gray, a giant *Artibeus* that ranges from southern Brazil to southern Paraguay (Handley, 1990). Remarkably, this taxon, which until very recently escaped the notice of all mammalogists, was recognized and named twice by John E. Gray: once in 1838 as *A. fimbriatus* and later, on a specimen label, as *A. grandis* (nomen nudum). The Spix specimen extends the range of *A. fimbriatus* northward in the coastal tropical rainforest belt to Bahia. The current status of *A. fimbriatus* in this region is unknown. North of São Paulo very little of the coastal forest has survived clearing. However, there are other specimens of *A. fimbriatus* from Bahia collected more recently than Spix (1823)—Museum of Comparative Zoology (Harvard) no. 197, alcoholic and skull (G. M. Allen, 1908), and Museu de Zoologia Universidade de São Paulo nos. 7395 and 7396, alcoholic and skull.

The confusion created by Spix's composite sample of *P. planirostre* has confounded mammalogists for more than 150 years. It was responsible, in large measure, for Andersen's (1908) failure to recognize *A. lituratus* as a distinct species as well as for his curious nomenclature and contorted reasoning that allied all of the large *Artibeus* of South America in two species, *A. jamaicensis* and *A. planirostris.*

REDESCRIPTION OF *PHYLLOSTOMA PLANIROSTRE* SPIX

Artibeus jamaicensis planirostris Spix

Phyllostoma planirostre Spix, 1823: 66 and pl. 36, fig. 1 (in part).
Arctibeus planirostris Gray, 1838: 487 (in part).
Ph[*yllostoma*]. *perspicillatum* Wagner, 1840: 403 (in part).
Artibeus [*Phyllostoma planirostre*] Peters, 1865: 587 (in part).
Artibeus planirostris Dobson, 1878: 515 (in part).
Artibeus planirostris planirostris Andersen, 1908: 237 (in part).
A[*rtibeus*]. *j*[*amaicensis*]. *planirostris* Hershkovitz, 1949: 447.

LECTOTYPE: Zoologische Staatssammlung Munich (ZSM) [65]/1903/9437, adult skin, skull, and partial skeleton, collected in 1818 or 1819, by J. B. R. von Spix, near Bahia, Brazil.

DISTRIBUTION: Northeastern Brazil: Coast

from Rio de Janeiro to Bahia, Pernambuco, and Maranhão, and, judging by the measurements of Willig (1983), nearby caatingas and cerrados of the interior of the Northeast. Larger, intergrading with *A. j. fallax* Peters, but still recognizable as *A. j. planirostris* south to Mato Grosso and eastern Paraguay.

DESCRIPTION: Size small for *A. jamaicensis* (forearm 56.5–63.1 mm, greatest length of skull 27.0–29.0 mm, maxillary toothrow length 9.6–10.8 mm); coloration pale brown, a little paler below; facial stripes obsolete or absent; fur short (6–8 mm); legs and interfemoral membrane practically naked; horseshoe of noseleaf free mediobasally. Skull broad, zygomata flaring, and postorbital wide; rostrum short, arched, and not inflated anterolaterally; supraorbital part of frontal sharp-edged and postorbital process well developed; ridge from postorbital process to sagittal crest usually well developed; narrowest point of frontals well behind postorbital processes. Dental formula 2/2—1/1—2/2—3/3 × 2 = 32.

COMPARISONS: *A. obscurus* Wied is sympatric with *A. j. planirostris* and resembles it in size, but is much darker colored (blackish) and has longer, softer fur; chin ornament with fewer, smaller warts; rostrum relatively longer, shallower, not so arched, and notably broader anteriorly; postorbital constriction more parallel sided and narrowest immediately behind postorbital processes; crests and processes not so well developed; 3rd upper molar often missing (Handley, 1990).

Compared with *A. j. planirostris,* the sympatric *A. fimbriatus* is much larger; has hairier extremities; horseshoe of noseleaf ridged at base and bound down mediobasally; longer, broader, shallower, flatter (less arched) rostrum; and poorly developed lachrymal and postorbital processes and ridges; and lacks M3.

SPECIMENS EXAMINED (National Museum of Natural History identified as USNM): *Artibeus jamaicensis planirostris:* BRAZIL: Bahia, Bahia (1, MCZ). Maranhão, Anilo (1, USNM); São Luiz (9, USNM). Pernambuco, Pernambuco (1, USNM; 3, BM); São Laurenco (6, BM). Rio de Janeiro (1, MCZ). *Artibeus fimbriatus:* BRAZIL: Bahia, "Bahia" (1, MCZ); "Salvador" (2, MZUSP). Plus 69 other specimens from southern Brazil and Paraguay (see Handley, 1990).

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The Systematic Status of *Dermanura concolor* (Peters, 1865) (Chiroptera: Phyllostomidae), with Description of a New Genus

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ABSTRACT

Dermanura concolor (Peters) was described in 1865 as a member of the large stenodermatine genus *Artibeus*. Andersen (1908) considered it to be allied with the larger species of that genus, but later authors (Cabrera, 1958; Husson, 1978; Handley, 1987) found it to be more closely related to the smaller forms. Owen (1987) concurred that *concolor* was more closely allied with the smaller species, to which he assigned the generic name *Dermanura*; nonetheless, he suggested inclusion of *concolor* within *Dermanura* only "until additional evidence is available."

In the present study, Owen's (1987) discrete-state character set was reanalyzed using Camin-Sokal parsimony for the dental characters. This analysis, using several outgroups, showed *concolor* to be more closely related to the "short-faced" stenodermatine species than to *Dermanura*. *Concolor* is not a natural member of the genus *Dermanura*. Because no generic name is available for this species, a new one is proposed in honor of Dr. Karl F. Koopman.

RESUMEN

Dermanura concolor (Peters) fue descrito en 1865 como miembro del enorme género *Artibeus*. Andersen en 1908 lo consideró aliado con las especies de mayor tamaño de este género. Posteriormente otros autores (Cabrera, 1958; Husson, 1978; Handley, 1987) encontraron una relación más estrecha con las especies más pequeñas. Owen (1987) confirmó que *concolor* es más afín con las especies de menor talla, a las cuales asignó el nombre genérico de *Dermanura*; sugiriendo la inclusión de *concolor* en el género *Dermanura* mientras "evidencia adicional es encontrada."

En el presente estudio, el grupo de caracteres discretos descritos por Owen (1987) fue reanalizado utilizando la parsimonia de Camin-Sokal para características dentarias. Este analisis, utilizando varios grupos ajenos al taxón reveló que *concolor* esta más estrechamente relacionado con las especies "cara-cortas" de los stenodermatines que a *Dermanura*. *Concolor* no es un miembro natural del género *Dermanura*. En ausencia de un nombre genérico para esta especie se propone uno en honor del Dr. Karl F. Koopman.

INTRODUCTION

In 1865, Peters described as *Artibeus concolor* a medium-sized, fruit-eating bat with three molar teeth both above and below, based on a specimen from Paramaribo, Suriname. Later, Andersen (1908), in the only published revisionary study of bats of the genus *Artibeus*, arranged *concolor* as allied to the larger species *A. planirostris* and *A. hirsutus*, and by inference ultimately to *A. jamaicensis* (including *lituratus* and several other larger species as now recognized), principally on the basis of 3/3 molars. Aside from having three molars in each jaw (the third considerably reduced in size but nonetheless a well-de-

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veloped tooth), Andersen noted that *A. concolor* was considerably smaller than other species or their supposed relatives that fell in that same category (he described it as "intermediate" in size between the smaller and larger taxa of *Artibeus* exclusive of *Enchisthenes hartii*), had a "peculiarly shortened" rostrum, and differed in other details of morphology from both large and small representatives of the genus. Andersen treated all *Artibeus*-like bats (again other than *Enchisthenes*) as members of single genus, even though the name *Dermanura* Gervais, 1855, was available for the smaller members of the assemblage.

For more than three-quarters of a century following Andersen's monographic treatment, *A. concolor* was more or less universally recognized as a distinct specific entity (see, for example, Cabrera [1958] and Husson [1978]), relatively rare in museum collections, but allied with the smaller *Artibeus* rather than the larger species of that group. Recently, Handley (1987) and Owen (1987) both have addressed the relationships of *concolor* in context with all other small *Artibeus*-like bats. The former author, following description of a new species, provided a synopsis of the "groups" of small taxa of the genus *Artibeus,* of which he recognized six; one of these contained only *concolor.*

Owen (1987), on the other hand, in a phylogenetic analysis of stenodermatine bats, concluded that the smaller species of *Artibeus* (sensu lato) actually represented a distinct genus, for which he employed the name *Dermanura.* Both *concolor* and *hartii* were included within *Dermanura,* although it was noted that the relationships of these two species to other members of the genus were "yet unclear." With this as a background, I here further consider the relationship of *concolor* to its reputed relatives. Although these analyses also are relevant to the status of *hartii,* that question is being addressed separately in a study by Joaquín Arroyo-Cabrales.

Materials and Methods

Phylogenetic analyses included all species determined to be in the same primary clade as *concolor* (Owen, 1987). These are the species of the genus *Dermanura* (including *Enchisthenes*) and the stenodermatine "short-faced" bats: genera *Pygoderma, Centurio, Phyllops, Ardops, Ariteus, Ametrida, Sphaeronycteris,* and *Stenoderma.* The one recognized species not included in the analysis is the recently described *Dermanura gnoma* (Handley, 1987; as *Artibeus gnomus*). For specimens examined, see Owen (1987: appendix I).

A series of 22 discrete-state characters was utilized for the analyses. These are listed and described in Owen (1987: table 1 and appendix II; the condition of both M3 and m3 was miscoded in the table, even though properly coded in the analyses). A detailed description of the additive binary coding and character rooting procedure was given by Owen (1987). The values for the 46 binary characters are listed in table 1 of this paper, and the characters are defined in the Appendix.

As outgroups for *Dermanura* and the short-faced bats, one member from each of two of the other three primary stenodermatine clades (Owen, 1987: fig. 17) was used. *Sturnira ludovici* was chosen to represent the *Sturnira* clade, and *Artibeus jamaicensis* was chosen to represent the primary clade of *Artibeus, Uroderma, Ectophylla, Platyrrhinus, Vampyrodes, Chiroderma,* and *Vampyressa.* (I follow Gardner and Ferrell [1990] in the use of *Platyrrhinus* rather than *Vampyrops.*) Another outgroup taxon (*Carollia brevicauda*) was chosen to represent the carolliine bats, a sister group of the stenodermatines (Hood and Smith, 1982). (I use "stenodermatines" to mean those genera that composed the recognized subfamily Stenodermatinae prior to Baker et al.'s [1989] revision of Phyllostomidae. Following Baker et al., the stenodermatines, along with the carolliines, compose the tribe Stenodermatini.) In each case, the species selected as an outgroup was thought to represent a relatively primitive morphotype within its clade. In order to determine the response to different outgroup taxa being used to root the trees, analyses were done using each of the outgroup species separately.

Many dental characteristics (e.g., loss of teeth) are known to evolve in parallel or convergent fashion among phyllostomids ("rampant parallelism"—Sluys, 1989). Consequently, these characters were subjected to Camin-Sokal parsimony in the analyses. This means that a forward step (e.g., reduction or

TABLE 1
Character State Values for Each of the 22 Taxa Examined in This Study
(1 = presence of the character state as defined in the Appendix)

Ametrida centurio	0001100010100110100110110011011110000010000000
Ardops nicholsii	0101000010110110000111010111011110010100000000
Ariteus flavescens	0001100010110110000111000011011111000100001100
Centurio senex	1001110011100110111111100011011111000100001011
Dermanura anderseni	0010001100100110000110110011110011000010001011
D. azteca	0100001100110110000110010011011011000000001011
D. cinerea	0000001100100110000110010111010011000000001011
D. concolor	0001000000100111000110011011011110001000000000
D. glauca	0010001100100110000110100010011011000000001110
D. hartii	0001101100110110000110110110011000000010000000
D. phaeotis	0110001100100110000110010111011011100000001011
D. tolteca	0110001100100110000110110111011011101000001011
D. watsoni	0110001100100110000110010010011011001000001110
Phyllops falcatus	0101100010110110000111010111011110101100000000
P. haitiensis	0101110010110110111111111011111111010110000000
P. vetus	0101100010110110000111010110011010000100000000
Pygoderma bilabiatum	0101100010000110000110010111011111010001001011
Sphaeronycteris toxophyllum	0101110010100110110111110011011110000011100010
Stenoderma rufum	0010000010100110100111000111011010001111110000
OUTGROUPS	
Artibeus jamaicensis	0001001100100110000110010011011111001000001110
Sturnira ludovici	0001100000111100000010100111000000100011000000
Carollia brevicauda	0000000000000000000000000000000000000000000000

loss of M3) is considered more likely to occur multiple times independently than to be reversed (the tooth to be "regained") in a lineage. Nondental characters (external and cranial) were subjected to strict parsimony in which reversals and convergences are considered to be equally likely.

Because several equally parsimonious trees were found in each analysis, a majority-rule consensus tree (Felsenstein, 1988) was computed for the trees resulting from analysis with each of the three outgroup taxa. Finally, an overall consensus tree was computed from these three consensus trees. Character states then were mapped onto this tree in order to evaluate the characteristics (synapomorphies) that define each clade.

In order to evaluate the supposition that the dental characters have evolved in a method concordant with Camin-Sokal parsimony, another set of analyses was conducted as just described, except that all characters were subjected to Wagner (strict) parsimony. All analyses were done using PHYLIP version 3.1 (Felsenstein, 1988).

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Dr. J. Knox Jones, Jr. made a substantial contribution to this paper by independently examining a number of specimens and by providing a large portion of the introductory and descriptive text. In fairness to Knox, it should be noted that he does not agree with the primary conclusions of this paper.

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RESULTS

The overall consensus of the three analyses using Camin-Sokal parsimony on the dental characters (fig. 1) indicates that the short-faced bats compose a monophyletic group, and that the genus *Dermanura* (exclusive of *concolor* and *hartii*) also is monophyletic. The species *concolor* is shown as a sister of the short-faced

bats, with *D. hartii* a sister of the *concolor* and short-faced group. Two of the three consensus trees (from the separate Camin-Sokal analyses, using different outgroups) show *concolor* as sister of the short-faced clade, and the third (with *Sturnira* as the outgroup) shows *concolor* as a member of that clade. Two of these three consensus trees show *hartii* to be the next sister taxon, whereas one (again with *Sturnira* as the outgroup) shows *Dermanura* (exclusive of *concolor* and *hartii*) as the next sister group, with *hartii* the sister of all other taxa in the study.

The overall consensus of the all-Wagner analyses is concordant with the Camin-Sokal analyses in showing *concolor* as sister of the short-faced clade (fig. 2). This tree differs from figure 1 in the placement of *hartii* (here placed among the short-faced bats) and in some relationships within the two larger groups. In each of the three consensus trees from the Wagner analyses, *concolor* is the sister taxon of the short-faced group.

DISCUSSION

The two overall consensus trees from the two parsimony algorithms are concordant with respect to a number of clades (figs. 1, 2). Both show *Dermanura* (exclusive of *concolor* and *hartii*) to be monophyletic. Both also show the short-faced bats as monophyletic (except that *hartii* is included in this clade in the Wagner results). It appears that the effect of imposing Camin-Sokal or Wagner parsimony on the dental characters is seen primarily with respect to the placement of *hartii* and some arrangements within *Dermanura*. In either case, the monophyly of *Dermanura* (sensu stricto) and the placement of *concolor* and *hartii* outside of that clade seem to be stable components of the analytic results.

In none of the most-parsimonious trees, using any of the three outgroups, for either type of analysis (Camin-Sokal or Wagner parsimony) was *concolor* shown to be a member of, or the immediate sister of, the other species of *Dermanura*. Based on these analyses of external, cranial, and dental characters, as well as the studies of Koop and Baker (1983) of isozymes and Tandler et al. (1986) of submandibular secretory granules, I conclude that *concolor* is not a natural member of the *Dermanura* group, and should no longer be recognized as congeneric with species therein, nor is it a member of any other genus-level group among the bats considered in this study and by Owen (1987). As no generic name is available for this species, I am pleased to propose the name below.

Koopmania, new genus

TYPE SPECIES: *Koopmania concolor* (Peters, 1865). The genus as currently conceived comprises only the type species, which is monotypic (Jones and Carter, 1976).

ETYMOLOGY: This taxon is named in honor of Dr. Karl F. Koopman, a man and scientist for whom I have the utmost admiration and respect. Karl's contributions to Neotropical bat systematics have been profound, and it is my privilege to count him as a friend and colleague.

GEOGRAPHIC DISTRIBUTION: Northern South America in the Guianas, southern Venezuela, southeastern Colombia, Amazonian Peru, and northern Brazil (Koopman, 1982).

DIAGNOSIS: Size medium, intermediate between species assigned to *Artibeus* and those assigned to *Dermanura* by Owen (1987); forearm, 43–52 mm (Handley, 1987); plagiopatagium attaching to metatarsal–phalangeal joint; females averaging larger than males (Eisenberg, 1989); facial stripes indistinct; molars 3/3, with m3 much smaller than in *hartii*; M1 with strongly developed hypocone; lower incisors forming a solid arcade; braincase highly vaulted, highest just anterior to midpoint; rostrum broad and short (shorter than in *Dermanura* species except *D. gnoma* [Handley, 1987]), with rostral shield well developed; rostrum distinctly dished in lateral view; mesopterygoid fossa broadly U-shaped; paraoccipital processes absent or indistinct; postpalatal shelf shorter than in *Dermanura*.

COMMENTS: Assuming figure 1 to be the working hypothesis of phylogenetic relationships among the species considered, I mapped character state changes onto this tree, again treating dental characters as Camin-Sokal parsimonious. The *Dermanura* clade is characterized by six character state changes (see Appendix). Absence of characters 3 and 4

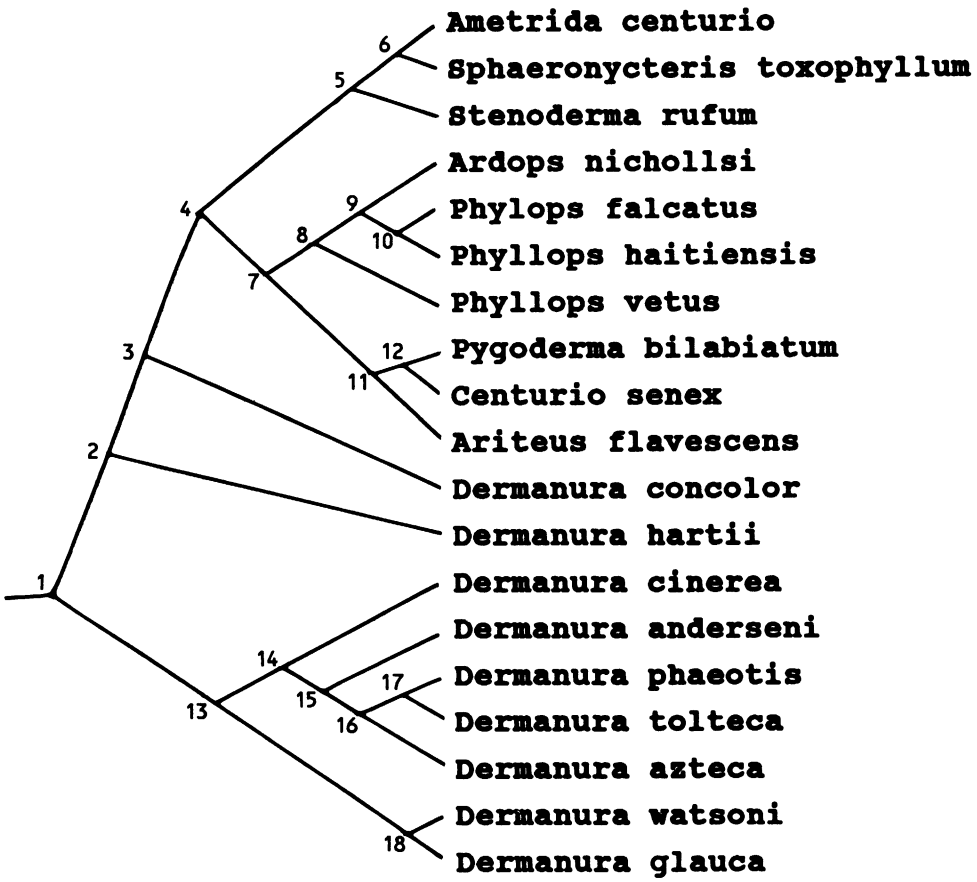

Fig. 1. Proposed phylogeny of species examined in this study. This consensus tree is derived from three analyses using Camin-Sokal parsimony on the dental characters and Wagner parsimony on the other characters. Estimated character state changes (with character state in parentheses for each character) for each node and species are: **1:** 30(1); **2:** 3(0), 4(1), 31(1); **3:** 7(0), 8(0), 28(1), 33(1); **4:** 9(1), 22(1); **5:** 17(1), 39(1); **6:** 5(1), 23(1), 32(1), 38(0); **7:** 5(1), 38(1); **8:** 2(1), 12(1), 26(1); **9:** 32(1); **10:** 35(1), 37(1); **11:** 32(1), 34(1), 43(1); **12:** 12(0), 45(1), 46(1); **13:** 4(0), 5(0), 33(1), 34(1), 43(1), 45(1); **14:** 28(1), 46(1); **15:** none; **16:** 2(1), 31(1); **17:** 3(1), 26(1), 35(1); **18:** 3(1), 28(0), 31(1), 44(1); *Ametrida centurio:* 22(0), 40(0), 41(0); *Sphaeronycteris toxophyllum:* 2(1), 6(1), 18(1), 40(1), 41(1), 45(1); *Stenoderma rufum:* 3(1), 4(0), 5(0), 24(0), 26(1), 37(1), 38(1), 40(1), 41(1), 42(1); *Ardops nichollsi:* 5(0), 36(1); *Phyllops falcatus:* none; *P. haitiensis:* 6(1), 17(1), 18(1), 19(1), 23(1), 29(1); *P. vetus:* 28(0); *Pygoderma bilabiatum:* 2(1), 11(0), 22(0), 24(1), 26(1), 36(1), 38(0), 40(1); *Centurio senex:* 1(1), 6(1), 10(1), 17(1), 18(1), 19(1), 23(1), 24(0); *Ariteus flavescens:* 12(1), 24(0), 44(1); *Dermanura concolor:* 5(0), 16(1), 25(1), 32(1), 37(1); *D. hartii:* 5(1), 12(1), 23(1), 26(1), 28(0), 39(1); *D. cinerea:* 3(0), 26(1); *D. anderseni:* 3(1), 23(1), 29(1), 39(1); *D. phaeotis:* none; *D. tolteca:* 23(1), 37(1); *D. azteca:* 3(0), 12(1); *D. watsoni:* 2(1), 37(1); *D. glauca:* 23(1), 24(0). Characters are listed and described in Appendix.

indicates a lengthening of the nose leaf (convergent in *Stenoderma, Ardops,* and *Koopmania*). Presence of character 33 reflects a reduction of M3 (convergent for the clade containing *concolor* and the short-faced bats); 34 a loss of M3 (convergent with *Ariteus, Pygoderma,* and *Centurio*); 43 the loss of a premolar; and 45 the reduction of m3 (convergent in *Sphaeronycteris, Pygoderma,* and *Centurio*).

The clade of *Dermanura hartii, Koopmania,* and the short-faced bats is characterized by a long nose leaf (characters 3 and 4; however, these characters map ambiguously in

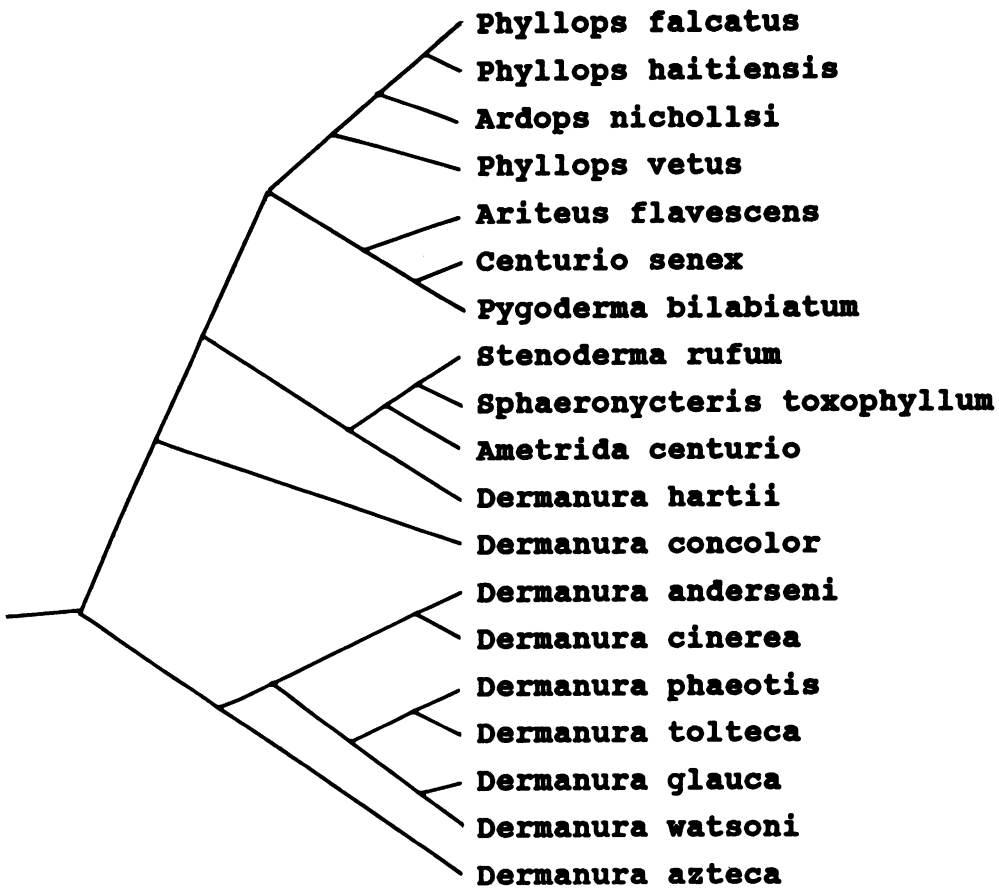

Fig. 2. Consensus tree derived from three analyses using Wagner parsimony on all characters.

several parts of the tree, and likely are not particularly informative) and a moderate development of the M1 hypocone (convergent with a majority of the *Dermanura* species). The clade containing *Koopmania* and the short-faced bats is defined by three-banded dorsal hair (character 7), loss of facial stripes (character 8), moderate basisphenoid pits (character 28, reversed in *Phyllops vetus* and convergent in most *Dermanura*), and reduction of M3 (33, noted earlier as convergent with the *Dermanura* clade).

Koopmania is characterized by loss of character 5 (i.e., increase in nose leaf length), attachment of the plagiopatagium to the metatarsal–phalangeal joint (16), loss of paraoccipital process (25), strong development of M1 hypocone (32), and loss of secondary foramen of the occipital condyle (37). The plagiopatagial and paraoccipital process conditions serve as synapomorphies that distinguish *Koopmania* from all other taxa within this evaluation. The others are convergent with various taxa on the tree (fig. 1).

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APPENDIX

The characters listed below were analyzed in this study. The 46 characters were derived by additive binary coding from the 22 multistate characters listed by Owen (1987: table 1 and appendix II). Two characters (1 and 10) are autapomorphic for *Centurio* and were not informative in these analyses.

1. Anterioproximal lobe on pinnae.
2. Lateral emargination of pinnae extending three-fourths of the ear length (versus one-half).
3. Nose leaf quite long (> 1½ times width).
4. Nose leaf shorter than in 3 (> width).
5. Nose leaf shorter than in 4 (length = width).
6. Nose leaf shorter than in 5 (length < width).
7. Two discrete bands on dorsal hair (versus three).
8. Facial stripes.
9. White shoulder patch.
10. Ribbed pattern on patagium mediad to fourth digit.
11. Uropatagium shorter than one-half the sacrum-to-calcar distance.
12. Uropatagia connected only adjacent to sacrum.
13. Uropatagia not connected.
14. Plagiopatagium attaches distally to tarsus.
15. Plagiopatagium attaches distally to metatarsus.
16. Plagiopatagium attaches distally to metatarsal–phalangeal joint.
17. Incisive foramen medium.
18. Incisive foramen small, anteriorly located.
19. Incisive foramen minute or absent.
20. Nasal septal foramen absent.
21. Hard palate extends no farther posterior to orbital anterior than palatal width.
22. Hard palate does not extend posterior to orbital anterior.
23. Hard palate posterior border squared (versus V-shaped).
24. Two parapterygoid foramina present (versus one).

25. Paraoccipital process absent (versus small).
26. Paraoccipital process enlarged (versus small).
27. Basisphenoid pits deep (versus exceptionally deep).
28. Basisphenoid pits moderately deep.
29. Basisphenoid pits shallow.
30. M1 hypocone a slight protuberance (versus absent).
31. M1 hypocone moderately developed.
32. M1 hypocone strongly developed.
33. M3 reduced (versus fully developed).
34. M3 absent.
35. Hypoglossal foramen absent (versus small).
36. Hypoglossal foramen medium (versus small).
37. Secondary foramen of occipital condyle absent.
38. Postglenoid foramen present.
39. External nares extend caudad so that bony palate clearly visible from dorsal view.
40. Rostrum flat or slightly troughed (versus dorsally convex).
41. Rostrum moderately troughed.
42. Rostrum strongly troughed.
43. Loss of lower premolar (from three to two).
44. Loss of lower incisor (from two to one).
45. m3 reduced (versus fully developed).
46. m3 absent.

Systematic Variation in the Megachiropteran Tube-nosed Bats *Nyctimene cyclotis* and *N. certans*

R. L. PETERSON[1,2]

ABSTRACT

Twenty-four adult specimens of *Nyctimene cyclotis* Andersen and 36 of *Nyctimene certans* Andersen were measured and analyzed using both univariate and multivariate statistical programs. The holotypes of both taxa were examined and measured (both skulls incomplete) and compared with complete specimens. The two species share dental, ear-shape, and pelage characteristics; they occur sympatrically and are shown to be distinct from each other and from other members of the genus when compared with *Nyctimene cephalotes* and *N. papuanus*.

INTRODUCTION

The primary objective of this study is to determine the taxonomic status of *Nyctimene cyclotis* and its relative *N. certans* and to clarify their systematic relation to other species.

Knud Andersen (1910: 623) described *Nyctimene cyclotis* as follows:

> Size small (forearms of type broken, estimated length 53 mm.); premolars and molars peculiarly short and broad, subcircular in outline (character particularly pronounced in p^4 and m^1, p_4 and m_1); m^1 reduced to about ⅔ or ¾ the size of p^4, m_1 slightly smaller than p_4; ears unusually broad, nearly as broad as long, and semicircularly rounded off above; back mottled with brownish tips to the hairs; a narrow spinal stripe along posterior half of back. Hab. New Guinea. *Type.* male ad. (al. and skull), Arfak Mts., N.W. New Guinea, collected by A. E. Pratt, B.M. 10.7.16.9.

Two years later, in his classic review of the Megachiroptera (Andersen, 1912b), the holotype of *N. cyclotis* was still the only known specimen, but Andersen elaborated on its pelage coloration and texture, pointing out that the fur is long and woolly with the length of the general mass about 9.5 mm and the longest hair 14 mm. He also provided available measurements for the holotype.

Unfortunately, the skull of the holotype is damaged, lacks the occipital region, and has missing teeth as well as a broken forearm. It is a fairly old specimen with well-worn dentition (photographed and measured; see "Systematic Summary").

To date the species has remained little known. Tate (1942) did not list either *N. cyclotis* or *N. certans* in his review of *Nyctimene*. Laurie and Hill (1954) listed it but also included *N. certans* as a subspecies without further comment. McKean (1972) provided measurements and comments for a single female specimen (CM2316) from Lake Kutubu (ca. 830 m), Papua. Koopman (1979, 1982) mentioned *N. cyclotis* without any new data. Smith and Hood (1981) reported two New Britain specimens from Warangoi, 4500 ft, East New Britain Province, from the collections of the Bernice P. Bishop Museum, Honolulu, Hawaii, but they did not encounter it during their study there. Smith and Hood (1983) figured BBM-NG 28398 of the Bishop Museum (their figs. 1C, 2C) and provided

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[2] Published posthumously without the benefit of revision by Randolph Peterson. Revisions were made by Judith L. Eger, Associate Curator, and Lorelie Mitchell, Departmental Associate, Department of Mammalogy, ROM. Reprint requests should be directed to Judith L. Eger.

general comments, particularly comparing it with *N. masala,* but gave no measurements or locality data for the figured specimen.

Nyctimene certans was described by Andersen (1912a: 95) as follows:

> Most nearly related to *N. cyclotis* (Arfak Mts.), but dentition much heavier and colour of fur much darker.
>
> Size as *N. cyclotis* or little larger (forearm of type 58 mm.); ears as in *cyclotis,* unusually broad, semicircularly rounded off above, and narrowly edged all round with yellow, this yellow edge interrupted here and there by the dark central colour of the conch breaking through to margin of conch. Molariform teeth, as in *cyclotis,* subcircular in outline, with m^1 and m_1 conspicuously smaller than, respectively, p^4 and p_4, but all teeth much heavier, particularly broader, than in the related species: p^3 (length and breadth) of type (between parentheses corresponding measurements of the type of *cyclotis,* for comparison) 2.2 × 2.1 (2.0 × 1.7), p^4 2.0 × 1.8 (1.8 × 1.6), m^1 1.8 × 1.6 (1.6 × 1.3), p_3 2.5 × 2.0 (2.3 × 1.7), p_4 2.3 × 2.0 (2.1 × 1.7), m_1 2.0 × 1.7 (1.9 × 1.5), m_2 1.3 × 1.2 (1.2 × 1.1). Colour of fur peculiarly mottled above, as in *N. cyclotis,* but much darker: individual hairs of back seal-brown at extreme base (for about 5 mm.), then very pale buffy wood-brown (for 5–6 mm.), with short (2 mm.) dark brown tips; the mottled appearance of the colour of the head and back due to the dark brown tips of the hairs being too short to cover completely the paler middle portion of the hairs; a narrow and somewhat ill-defined dark brown spinal stripe along posterior half of back; breast and belly pale greyish drab in centre, flanks fawn.
>
> Type, skin and skull of an adult (unsexed), Mount Goliath, Dutch New Guinea, 20 Jan, 1911, collected by A. S. Meek, B.M. no. 11.11.29.1. Two other specimens from the Upper Aroa River, British New Guinea, are in the collection of the British Museum.

Later in the same year Andersen (1912b) virtually repeated the original description as an addendum in the "Catalogue" (p. 828), but added wing and foot measurements.

The skull of the holotype is badly damaged (see "Systematic Summary"). The measurements of the metacarpals are comparatively short, suggesting that it might be a subadult. The heavy dentition is also consistent with that of an unworn subadult (see figs. 1, 2 for *N. cyclotis*). The length of the mandible exceeds all *N. cyclotis* measured to date. A direct comparison of the holotypes of both taxa with ROM 94059 (fig. 3) indicated that the latter should be referred to as *Nyctimene certans.*

Because Laurie and Hill (1954) treated *N. certans* as a subspecies of *N. cyclotis,* subsequent authors have done likewise, but apparently no additional specimens have been referred to this taxon.

Materials and Methods

This study was carried out using a Compaq Deskpro 286 (70-megabyte hard disk; 1 megabyte RAM and a 20 × 20 Bernoulli Box added) and a Compaq Portable 386/20 (100-megabyte hard disk; 4 megabytes RAM and interfaced with calipers). Data entry and manipulation were done utilizing a caliper interface and a menued series of programs written for me by Jon Planck of Limnoterra, Kitchener, Ontario. These include programs that read measurement data files (.MTS) and convert the data to files formatted in a style acceptable by various statistical programs. Measurement files are formatted using "prompt files" (.PMT). The prompt file for *Nyctimene* is shown in table 1 as the left-hand column of data codes; the measurements taken (all in millimeters) and those used in the statistical analyses are listed and defined (*) in table 1. Data from the measurement files are transferred to Lotus 1-2-3 spreadsheet files (Lotus Development Corp.) for a preliminary review. Specimens are arranged in rows, with catalogue numbers read from the .MTS file, and variables in columns. For each variable the column ends with a calculation of the mean ($\bar{x}$), standard deviation (SD), variance (Var.), minimum, maximum, and N (number of specimens). See tables 2, 4, and 5.

Analyses included only complete adult specimens. Tests for sexual dimorphism showed no consistent significant differences, thus the sexes were combined.

As indicated above, *Nyctimene cyclotis* (NCYL) and *N. certans* (NCTN) share a number of distinctive characters, particularly the molariform dentition, in which the width across the upper third premolars is unusually broad, often exceeding the breadth across the last molars. *N. certans* is generally larger and appears to be restricted to rather high elevations, usually 1200 (one at 780, others 1220–3000) meters above sea level. *N. cyclotis* occurs from sea level to about 1500 meters. The two species have been collected sympatrically in at least four locations.

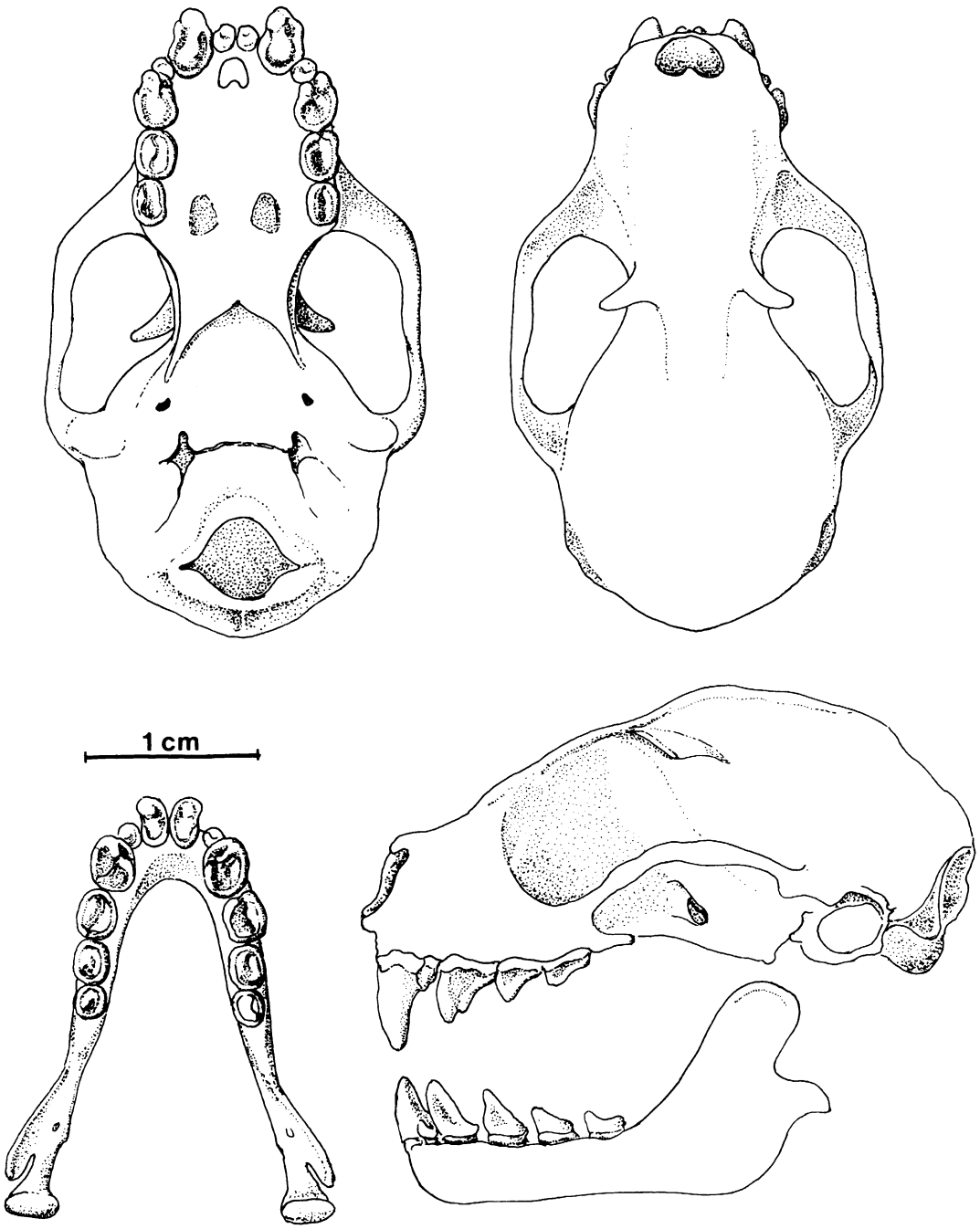

Fig. 1. Cranial drawings of *Nyctimene cyclotis,* BBM-NG 29062, subadult male from Big Wau Creek Ridge, 5 km SE Wau, Morobe District, Papua. Dorsal, ventral, and lateral views; drawn from photographs.

To provide a basis for comparison with other species, two additional taxa have been added to the following analyses. A sample of 37 specimens of *N. papuanus* Andersen, 1910 (NPAP), ranging from West Irian to Solomon Islands, is broadly sympatric with, and only slightly smaller than, *N. cyclotis.* It is of interest that the holotype of *N. albiventer minor*

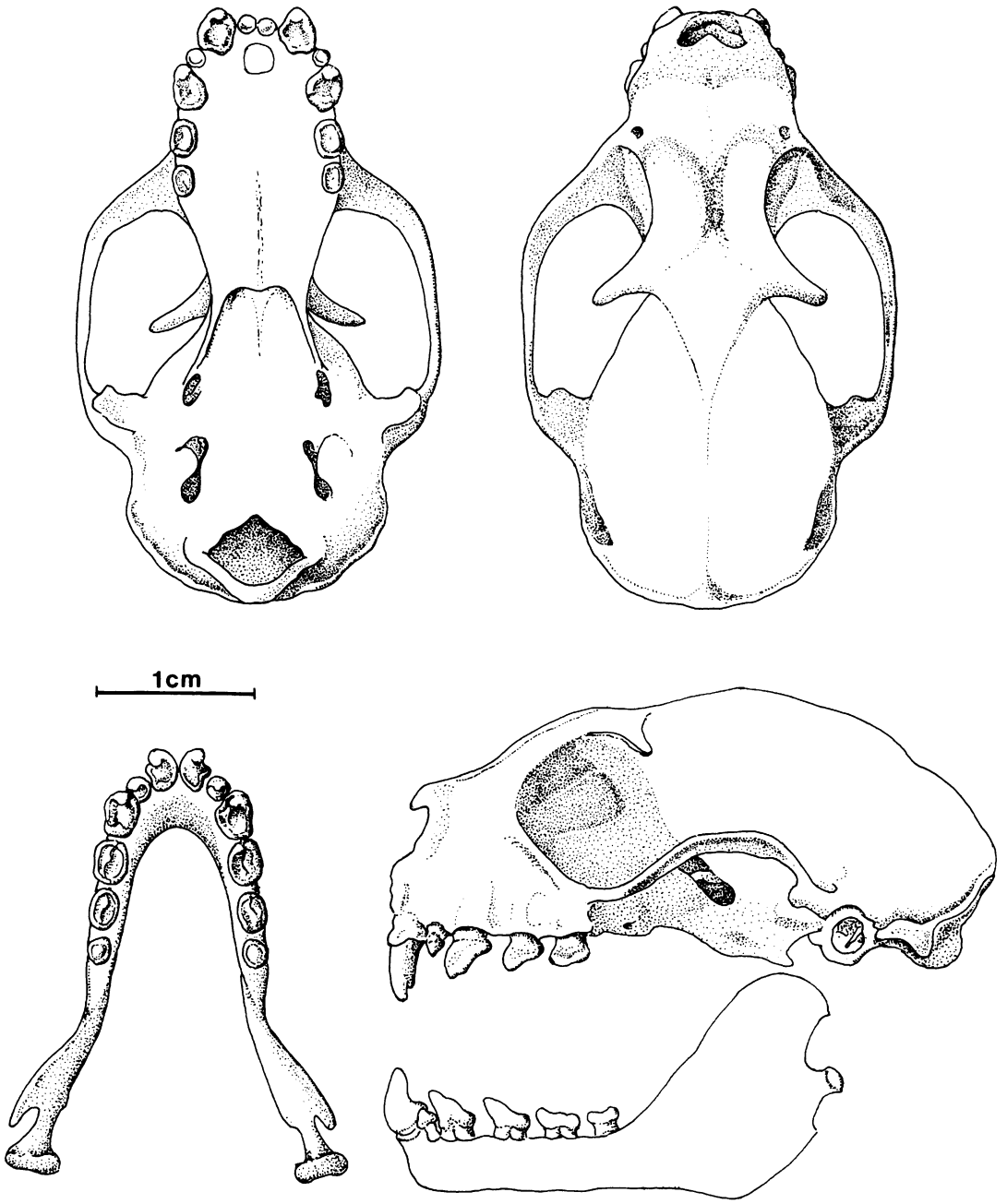

Fig. 2. Cranial drawings of *Nyctimene cyclotis,* BBM-NG 28396, adult female from the south slope of Mt. Missim, Morobe District, Papua. Dorsal, ventral, and lateral views; drawn from photographs.

(Phillips, 1968) falls within the *N. papuanus* population that appears to be distinct from *N. albiventer, draconilla, minutus,* and *varius.*

The second taxon added for comparison is *N. cephalotes* (Pallas, 1767) (NCEP), which is represented in this study by two topotype specimens from Ambon and 21 specimens from Sulawesi. Although it is the first named species of the genus, this taxon is still poorly understood (see Smith and Hood, 1983; Heaney and Peterson, 1984). Its relationship to

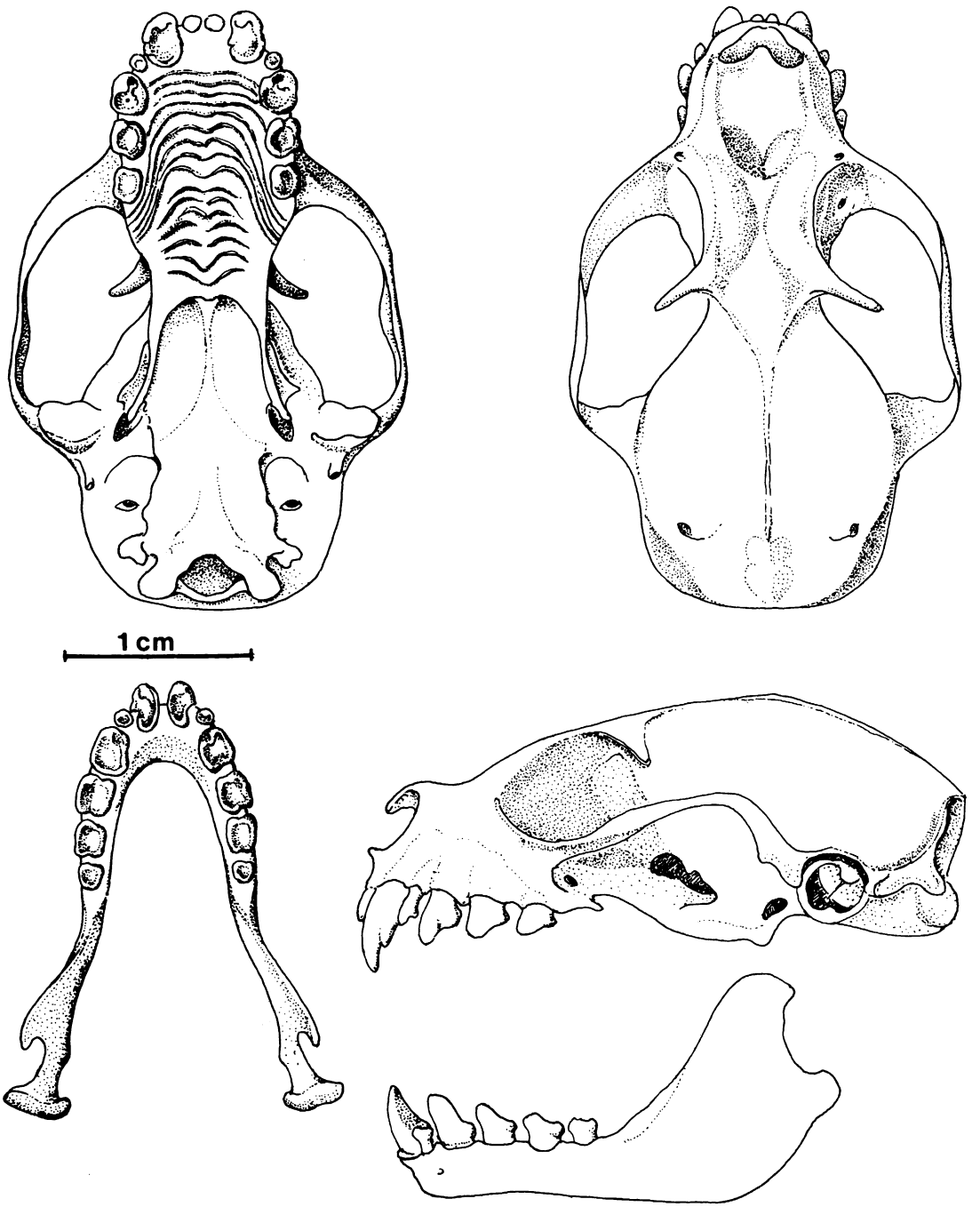

Fig. 3. Cranial drawings of *Nyctimene certans,* ROM 94059, adult male from Aiyura, Bismarck Range, Papua. Dorsal, ventral (with soft palate), and lateral views.

N. vizcaccia and to *N. robinsoni* requires further study. *N. cephalotes* has a skull of similar length to *N. certans,* but is generally larger in most other characters.

A hierarchical cluster analysis (Pimental and Smith, 1986) of my entire *Nyctimene* and *Paranyctimene* files confirmed the distinctive clustering of the above four taxa.

TABLE 1

Data Recorded in *Nyctimene* Measurement Files
(* indicates variable used in statistical analyses)

CAT NO	Catalogue number
SEX	F, M, or U
COLL	Collection
NS	Nature of specimen; A/S = alcoholic + skull; SS = skin and skull, etc.
AGE	A = adult; SA = subadult; JUV = juvenile
DATE	Date of collection
LOC	Locality collected
TL	Total length (head and body plus tail)
TV	Tail length
HF	Hind foot length (includes claws)
EAR-L	Ear length
EAR-W	Ear width
WT	Weight (grams)
WS	Wing span
NOTES	[All measurements in millimeters]
TIBI	Tibia length
FA*	Forearm length
D2M*	Second digit metacarpal length (includes flexed wrist)
D21P	Second digit first phalanx length
D22P	Second digit second phalanx length
D3M*	Third digit metacarpal length (includes flexed wrist)
D31P*	Third digit first phalanx length
D32P	Third digit second phalanx length
D4M*	Fourth digit metacarpal length (includes flexed wrist)
D41P*	Fourth digit first phalanx length
D42P	Fourth digit second phalanx length
D5M*	Fifth digit metacarpal length (includes flexed wrist)
D51P*	Fifth digit first phalanx length
D52P	Fifth digit second phalanx length
GL*	Greatest length of skull
CBL*	Condylobasal length
PALL*	Incisive palatal length
ZYGO*	Zygomatic breadth
MAST*	Mastoid breadth
BBC*	Breadth of braincase
HBC*	Height of braincase
ROSL	Rostrum length; rim of orbit to rim of nasal aperture
IOW	Interorbital breadth
PCP	Breadth across postorbital process
POC	Least postorbital constriction breadth
M1M1*	Breadth across first upper molars (crowns)
P3P3*	Breadth across third upper premolars (crowns)
C–M1*	Length front of upper canine to rear of first molar (crowns)
CCU*	Breadth across upper canines (crowns)
CIMA	Condyloincisive length of paired mandibles
GLM*	Condyloincisive length of one mandible
CM2L*	Length front of lower canine to rear of second molar (crowns)
CCL	Breadth across lower canines (crowns)
P3P3L*	Breadth across lower canines (crowns)
HTCP*	Height of coronoid process
DPF	Dorsal profile of frontal (coded description)
UPM	Upper premolars (coded description)
UM1	Upper molar (coded description)
LPM	Lower premolars (coded description)
LM	Lower molars (coded description)
OTU	Four-letter OTU code

Means were calculated for each sample after characters had been standardized across samples. Student-Newman-Keuls multiple-range tests were done on 23 variables. OTUs were ordinated using nonmetric multidimensional scaling (NT-SYS; Rohlf, 1988). To compare relationships within and among these *Nyctimene* OTUs, they were analyzed using discriminant function analysis (Biostat II; Pimental and Smith, 1986).

Acknowledgments

Thanks to the curatorial staff of the following collections, 459 specimens of *Nyctimene* and 12 of *Paranyctimene* have been examined, measured, and added to my data files:

AMNH	American Museum of Natural History, Karl Koopman
ANSP	Academy of Natural Sciences, Philadelphia, Charles L. Smart
AUM	Australian Museum, Sydney, Linda Gibson
CSIRO	Australian National Wildlife Collection, J. H. Calaby and G. C. Richards
BBM	Bernice P. Bishop Museum, Honolulu, Alan C. Ziegler
BM(NH)	British Museum (Natural History), J. E. Hill
DMNH	Delaware Museum of Natural History, J. DuPont
LACM	Los Angeles County Museum, Sarah George

TABLE 2
Subadult Measurements Compared With Those of Adults of *Nyctimene cyclotis* and *N. certans*

	N. cyclotis				*N. certans*			
	Subadults (N = 6)		Adults (N = 24)		Subadults (N = 4)		Adults (N = 36)	
	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.
FA	55.38	53.5–56.3	58.85	55.2–61.5	57.93	56.0–58.8	61.67	58.7–66.7
D2M	26.98	24.0–29.7	30.45	28.3–33.0	28.98	27.9–29.5	31.49	29.6–34.3
D3M	37.97	37.0–39.5	41.99	39.5–44.3	40.60	40.2–41.3	43.58	41.0–48.2
D31P	29.68	28.0–31.8	31.53	29.0–33.9	31.45	31.1–32.0	34.88	31.9–39.1
D4M	35.05	33.0–36.7	39.02	36.5–41.4	38.05	37.5–38.7	40.84	38.4–44.6
D41P	23.13	22.9–23.3	23.71	21.1–26.5	24.05	22.8–24.6	26.73	24.8–29.7
D5M	37.03	33.5–39.8	40.87	37.0–43.9	38.05	37.2–38.8	41.42	38.4–46.0
D51P	19.23	17.8–20.7	20.62	18.5–22.5	21.10	19.3–22.9	23.50	21.5–26.5
GL	27.98	27.5–28.7	29.04	28.0–30.2	30.03	29.6–30.2	31.02	30.0–32.8
CBL	26.17	25.4–26.7	27.35	26.5–28.2	28.18	27.8–28.6	29.37	28.5–31.0
PALL	12.30	11.8–12.5	13.01	12.2–13.9	13.10	12.9–13.2	13.80	13.1–14.8
ZYGO	17.48	16.9–18.0	18.67	17.4–20.0	18.90	17.7–20.1	19.49	18.5–20.7
MAST	12.43	12.0–12.9	12.60	11.7–13.3	12.60	12.3–13.0	13.00	12.4–13.8
BBC	12.58	12.3–13.3	12.56	11.8–12.9	12.78	12.5–13.2	13.11	12.4–13.8
HBC	9.65	9.2–10.0	9.74	9.1–10.4	9.95	9.4–10.3	10.31	9.6–11.0
M1M1	8.75	8.0–9.1	8.62	7.8–9.3	9.23	8.3–9.7	9.39	8.8–10.4
P3P3	8.70	8.1–9.5	8.41	7.9–8.9	9.00	8.4–9.2	9.26	8.7–9.8
C–M1	9.37	9.0–9.7	9.41	8.6–10.1	9.68	9.3–9.8	9.74	8.9–10.4
CCU	6.23	6.0–6.7	5.96	5.6–6.5	6.28	5.9–6.5	6.29	5.9–6.8
GLM	20.75	20.0–21.5	21.54	20.8–22.1	22.10	21.8–22.7	22.94	22.0–24.4
CM2L	10.70	10.1–11.2	10.81	10.0–11.4	11.03	10.3–11.5	11.26	10.5–12.0
P3P3L	7.12	6.8–7.5	6.96	6.5–7.4	7.48	6.9–7.8	7.58	6.9–8.3
HTCP	10.42	9.6–11.2	11.26	10.5–12.3	11.33	10.7–11.9	12.17	10.4–13.4

QM Queensland Museum, Brisbane, R. E. Molnar
RMNH Rijksmuseum van Natuurlijke Historie, C. Smeenk
ROM Royal Ontario Museum, Judith Eger, Nancy Grepe, Jim Borack, Lilian Lortie, Sophie Poray, and Susan Woodward
SAM South Australia Museum, Adelaide, Katherine Kemper
UMMZ University of Michigan, Museum of Zoology, L. R. Heaney
USNM U.S. National Museum of Natural History, C. O. Handley, Don Wilson, and A. Gardner

I have been accumulating data on the genus *Nyctimene* for a number of years and have had valuable assistance from M. B. Fenton, James Knowles, Cory Goldman, Michael Brown, Janet Cooper, Susan Woodward, and Burton Lim. Sophie Poray prepared the illustrations. Since my retirement, I have had the invaluable, competent, and dedicated voluntary assistance of Lorelie Mitchell, who, in addition to calling on her professional experience as a D.V.M., has become a keen expert on computers and statistical programs as well as on bat morphology. I also gratefully acknowledge the support of operating grant A2385 of the National Sciences and Engineering Research Council of Canada.

RESULTS

Age Variation

Volant subadults are characterized by incompletely fused joints between the wing bones and by relatively short metacarpals in relation to the length of the forearm. My measurements include the flexed wrist, whereas measurements published by Andersen (1912b) probably do not. Limited samples of subadults are compared with adults of both *N. cyclotis* and *N. certans* in table 2. The rapidly growing wing elements during a relatively short time period, and the random distribution of relative ages represented within the sample, make the calculated means of

TABLE 3

Nonsignificant Subsets as Determined by a Student-Newman-Keuls Multiple-range Test for *Nyctimene papuanus* (NPAP; N = 37), *N. cyclotis* (NCYL; N = 24), *N. certans* (NCTN; N = 36), and *N. cephalotes* (NCEP; N = 24)

Variable	OTU	$\bar{x}$	Subsets	Variable	OTU	$\bar{x}$	Subsets
FA	NPAP	56.85	I	MAST	NPAP	12.39	I
	NCYL	58.85	I		NCYL	12.60	I
	NCTN	61.67	I		NCTN	13.00	I
	NCEP	65.21	I		NCEP	13.20	I
D2M	NPAP	29.88	I	BBC	NPAP	12.38	I
	NCYL	30.45	I		NCYL	12.58	I
	NCTN	31.49	I		NCEP	12.89	I
	NCEP	32.33	I		NCTN	13.11	I
D3M	NPAP	41.66	I	HBC	NCYL	9.74	I
	NCYL	41.99	I		NPAP	9.82	I
	NCTN	43.58	I		NCTN	10.31	I
	NCEP	46.54	I		NCEP	11.39	I
D31P	NPAP	30.28	I	M1M1	NPAP	8.44	I
	NCYL	31.53	I		NCYL	8.62	I
	NCEP	33.77	I		NCEP	9.20	I
	NCTN	34.88	I		NCTN	9.39	I
D4M	NPAP	38.76	I	P3P3	NPAP	7.51	I
	NCYL	39.02	I		NCEP	8.02	I
	NCTN	40.84	I		NCYL	8.41	I
	NCEP	42.90	I		NCTN	9.26	I
D41P	NPAP	22.39	I	C–M1	NCYL	9.41	I
	NCYL	23.71	I		NPAP	9.52	I
	NCEP	25.50	I		NCTN	9.74	I
	NCTN	26.73	I		NCEP	10.59	I
D5M	NCYL	40.87	I	CCU	NPAP	5.55	I
	NPAP	41.04	I		NCEP	5.94	I
	NCTN	41.42	I		NCYL	5.96	I
	NCEP	45.75	I		NCTN	6.29	I
D51P	NPAP	18.74	I	GLM	NPAP	20.90	I
	NCYL	20.62	I		NCYL	21.54	I
	NCEP	21.43	I		NCEP	22.90	I
	NCTN	23.50	I		NCTN	22.94	I
GL	NPAP	28.48	I	CM2L	NPAP	10.77	I
	NCYL	29.04	I		NCYL	10.81	I
	NCTN	31.02	I		NCTN	11.26	I
	NCEP	31.17	I		NCEP	11.80	I
CBL	NPAP	26.78	I	P3P3L	NPAP	6.34	I
	NCYL	27.35	I		NCEP	6.82	I
	NCEP	29.21	I		NCYL	6.96	I
	NCTN	29.37	I		NCTN	7.57	I
PALL	NCYL	13.01	I	HTCP	NPAP	11.09	I
	NPAP	13.25	I		NCYL	11.26	I
	NCTN	13.80	I		NCTN	12.17	I
	NCEP	14.49	I		NCEP	12.99	I
ZYGO	NPAP	18.44	I				
	NCYL	18.67	I				
	NCTN	19.49	I				
	NCEP	19.89	I				

TABLE 4
Sample Statistics for *Nyctimene cyclotis* and *N. certans*

	N. cyclotis (N = 24)				*N. certans* (N = 36)			
Char.	$\bar{x}$	SD	Var.	Min.–max.	$\bar{x}$	SD	Var.	Min.–max.
FA	58.85	1.623	2.636	55.2–61.5	61.67	2.015	4.059	58.7–66.7
D2M	30.45	1.270	1.612	28.3–33.0	31.49	1.176	1.383	29.6–34.3
D3M	41.99	1.197	1.433	39.5–44.3	43.58	1.543	2.381	41.0–48.2
D31P	31.53	1.202	1.445	29.0–33.9	34.88	1.469	2.157	31.9–39.1
D4M	39.02	1.348	1.817	36.5–41.4	40.84	1.432	2.051	38.4–44.6
D41P	23.71	1.199	1.438	21.1–26.5	26.73	1.245	1.551	24.8–29.7
D5M	40.87	1.806	3.261	37.0–43.9	41.42	1.610	2.591	38.4–46.0
D51P	20.62	1.161	1.347	18.5–22.5	23.50	1.314	1.728	21.5–26.5
GL	29.04	0.607	0.369	28.0–30.2	31.02	0.595	0.354	30.0–32.8
CBL	27.35	0.452	0.204	26.5–28.2	29.37	0.545	0.297	28.5–31.0
PALL	13.01	0.460	0.212	12.2–13.9	13.80	0.436	0.191	13.1–14.8
ZYGO	18.67	0.669	0.448	17.4–20.0	19.49	0.449	0.202	18.5–20.7
MAST	12.60	0.336	0.113	11.7–13.3	13.00	0.335	0.112	12.4–13.8
BBC	12.56	0.250	0.062	11.8–12.9	13.11	0.323	0.105	12.4–13.8
HBC	9.74	0.351	0.123	9.1–10.4	10.31	0.336	0.113	9.6–11.0
M1M1	8.62	0.335	0.112	7.8–9.3	9.39	0.399	0.159	8.8–10.4
P3P3	8.41	0.285	0.081	7.9–8.9	9.26	0.319	0.102	8.7–9.8
C–M1	9.41	0.401	0.161	8.6–10.1	9.74	0.274	0.075	8.9–10.4
CCU	5.96	0.229	0.052	5.6–6.5	6.29	0.226	0.051	5.9–6.8
GLM	21.54	0.363	0.132	20.8–22.1	22.94	0.493	0.243	22.0–24.4
CM2L	10.81	0.360	0.129	10.0–11.4	11.26	0.350	0.122	10.5–12.0
P3P3L	6.96	0.234	0.055	6.5–7.4	7.58	0.298	0.088	6.9–8.3
HTCP	11.26	0.557	0.310	10.5–12.3	12.17	0.673	0.453	10.4–13.4

the subadults only approximate. In the wing elements of subadults, the upper end of the observed range tends to approach or slightly exceed the lower limits of the observed range for adults.

The general cranial development with age is essentially similar to that of *N. rabori* as reported by Heaney and Peterson (1984) and illustrated in their figure 4. In the younger ages, the sequence of fusion of the nasal and basal sutures (as they illustrated) provides a relative index to the age of subadults. As with many bats, subadults tend to have a greater downward deflection of the basicranial axis of the occiput that shifts to a more horizontal level as elongation of the braincase proceeds with maturity (compare figs. 1 and 2).

Subadults have unworn teeth of maximum size, as shown in figure 1. With wear, there is a marked change in width and space between the molariform teeth (fig. 2). As indicated in table 2, the means for the widths of the dentition of subadults (as represented by M1M1, P3P3, CCU, and P3P3L) of *N. cyclotis* are actually greater than those for the adults. Comparable means for the four *N. certans* subadults are consistently less than for the adults. In general, the relatively broad, unworn molariform teeth of subadults undergo steady wear with age, resulting in changes in the relative shapes of the occlusal surfaces, as well as a reduction in size of individual teeth and in the overall dental arcade measurements, particularly in width dimensions. The heavier, particularly broader, teeth ascribed by Andersen (1912a, 1912b) as distinguishing *N. certans* from *N. cyclotis* appear to be only a product of age differences between the two holotypes.

Univariate Analyses

The variables measured were examined individually to check on amount of variability exhibited and possible correlation with either sex or age. A suite of 23 variables was then selected as best representing the observed variations (table 1).

The results of univariate Student-Newman-Keuls multiple-range tests (Pimental and Smith, 1986) are summarized in table 3. For 7 of the 23 variables, all means were signif-

TABLE 5
Sample Statistics for *Nyctimene papuanus* and *N. cephalotes*

	N. papuanus (N = 37)				*N. cephalotes* (N = 24)			
Char.	$\bar{x}$	SD	Var.	Min.–max.	$\bar{x}$	SD	Var.	Min.–max.
FA	56.85	1.662	2.762	53.5–61.1	65.21	2.082	4.335	61.2–69.5
D2M	29.88	1.613	2.603	26.6–33.6	32.33	1.653	2.733	28.4–36.4
D3M	41.66	1.380	1.905	39.2–44.4	46.54	2.102	4.420	41.5–50.7
D31P	30.28	1.088	1.183	28.5–32.3	33.77	1.101	1.211	31.9–36.0
D4M	38.76	1.185	1.404	36.4–41.1	42.90	1.735	3.012	40.0–45.6
D41P	22.39	1.026	1.052	20.0–24.6	25.50	1.100	1.210	23.9–27.9
D5M	41.04	1.749	3.057	37.7–44.4	45.75	1.903	3.621	41.6–49.5
D51P	18.74	0.919	0.845	16.6–20.1	21.43	1.155	1.333	19.6–24.3
GL	28.48	0.496	0.246	27.5–29.8	31.17	0.981	0.963	29.5–33.4
CBL	26.78	0.474	0.225	25.5–27.7	29.21	0.952	0.907	28.0–31.1
PALL	13.25	0.468	0.219	12.3–14.1	14.49	0.663	0.440	13.3–15.6
ZYGO	18.44	0.399	0.159	17.7–19.2	19.89	0.969	0.938	18.3–22.1
MAST	12.39	0.316	0.100	11.5–13.0	13.20	0.543	0.295	12.1–13.9
BBC	12.38	0.340	0.116	11.6–12.9	12.89	0.497	0.247	12.0–13.7
HBC	9.82	0.301	0.090	9.1–10.4	11.39	0.751	0.564	9.6–12.8
M1M1	8.44	0.162	0.026	8.2–8.8	9.20	0.411	0.169	8.4–10.0
P3P3	7.51	0.204	0.042	7.1–7.8	8.02	0.291	0.085	7.4–8.4
C–M1	9.52	0.417	0.174	8.3–10.4	10.59	0.337	0.114	9.9–11.1
CCU	5.55	0.216	0.047	5.1–6.0	5.94	0.258	0.067	5.4–6.4
GLM	20.90	0.340	0.116	20.3–21.5	22.90	0.729	0.531	21.8–24.4
CM2L	10.77	0.399	0.159	9.9–11.5	11.80	0.347	0.120	11.2–12.4
P3P3L	6.34	0.227	0.052	6.0–6.9	6.82	0.239	0.057	6.4–7.4
HTCP	11.09	0.666	0.444	9.7–12.4	12.99	0.485	0.235	12.0–13.7

icantly different. The means of NCYL (*N. cyclotis*) and NCTN (*N. certans*) were significantly different from each other in 22 of 23 variables (all except D5M). There was no overlap in the condylobasal length of the skull (CBL) between these two species.

Comparing NCYL with NPAP (*N. papuanus*), the two share the same subsets in wing measurements D2M, D3M, D4M, and D5M, but are significantly different in D31P, D41P, and D51P. In cranial measurements the two OTUs also share common subsets in PALL, ZYGO, BBC, HBC, C–M1, CM2L, and HTCP, but are significantly different in all others.

Comparing NCTN with NCEP (*N. cephalotes*), the two share the same subsets only in GL, CBL, and GLM.

Sample statistics for NCYL and NCTN are given in table 4 and for NPAP and NCEP in table 5.

Multivariate Analysis

Results of the nonmetric multidimensional scaling analysis indicate that *Nyctimene cyclotis* and *N. certans* are morphologically very different on all three axes (fig. 4). With only four OTUs in the analysis, all the variance is explained by three axes. *Nyctimene papuanus* is the smallest species and *N. cephalotes* the largest. The minimum spanning tree distances (Euclidean distances) show a greater distance between *N. certans* and *N. cyclotis* than between *N. certans* and *N. cephalotes,* or *N. cyclotis* and *N. papuanus.*

Multivariate analysis of variance indicates that statistically significant differences exist among samples (F transformation of Wilk's lambda statistic = 22.797, df = 69 and 284, P = 0.0000). Classification of individual specimens resulted in 100 percent correct classification. A plot of individual specimens on the first and second canonical axes is shown in figure 5. In this analysis, *N. cyclotis* and *N. certans* are as different from each other as either is from *N. cephalotes.* Three canonical axes provide significant discrimination among the four groups, and the first two summarize 98 percent of the among-group differences (table 6). The following variables contribute to discrimination on the first canonical axis:

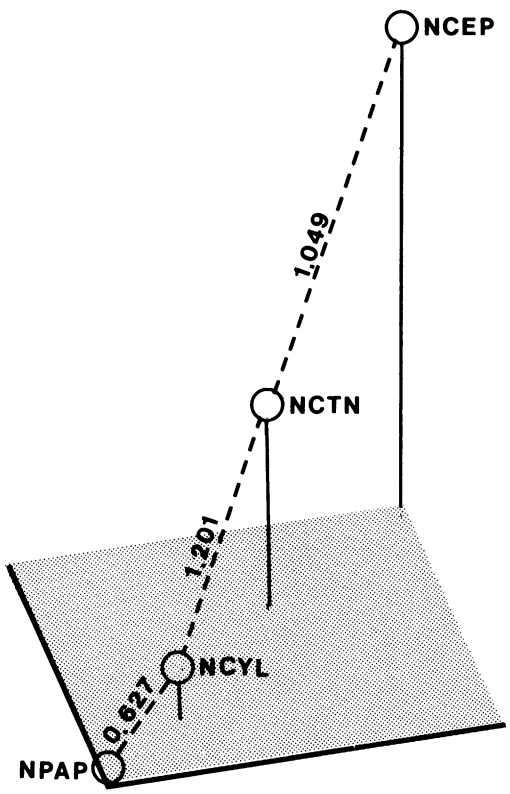

Fig. 4. Three-dimensional plot of nonmetric multidimensional scaling of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes,* with minimum spanning tree superimposed and Euclidean distances added.

fourth and fifth digit metacarpals, first phalanges of third and fifth digits, palatal length, zygomatic width, width across the first molars, and width across the premolars. Differentiation on the second axis is accounted for by length of forearm, condylobasal length, breadth of braincase, and height of braincase (table 7).

SYSTEMATIC SUMMARY

Nyctimene cyclotis Andersen, 1910

Nyctimene cyclotis Andersen, 1910: 623.

HOLOTYPE: Old adult male in alcohol with skull removed, BM(NH) 10.7.16.9, obtained by A. E. Pratt (unknown date) from Arfak Mountain, West Irian. Skull missing basioccipital region, right zygoma, right and left fourth upper premolars, and right upper molar. Dentition heavily worn.

MEASUREMENTS OF HOLOTYPE: Length of tail, 22.5; length of hind foot, 13.5; length of ear, 14.0; length of tibia, 21.5; length of forearm, ca. 54.5; length of metacarpals: second digit, 28.0; third digit, 40.0; fourth digit, 37.0; fifth digit, 38.2; length of first phalanges: third digit, 30.5; fourth digit, 24.5; fifth digit, 20.5; length of palate, 12.8; upper canine–molar length, 9.2; width across upper canines, 5.7; lower canine–molar length, 10.5; width across lower third premolars, 6.7; condyloincisive length of mandible, 21.5.

DISTRIBUTION: Mainland New Guinea (West Irian and Papua) and New Britain Island (see fig. 6 and "Specimens Examined" below).

COMPARISONS: Externally *Nyctimene cyclotis* and *N. certans* share many features, including long and woolly fur and relatively short and broad ears. Cranially, both are "wide-mouthed," with broad, rounded molariform teeth. The greater width across the upper third premolars in relation to the width across the molars is perhaps the unique shared characteristic that distinguishes these two taxa from all others of the genus.

In general, *N. cyclotis* is slightly smaller than *N. certans* and has a shorter (CBL = 26.5–28.2 versus 28.5–31.0 for NCTN), relatively broader skull with a more evenly rounded dorsal profile (compare figs. 1, 2 with fig. 3). For detailed comparison of individual characters, see tables 3 and 4.

Compared with *N. papuanus, N. cyclotis* is readily distinguished by the dental features described above, by its longer fur and broader ears, and by other characters shown in table 3.

Compared with *N. cephalotes, N. cyclotis* is also distinguished by its dentition and external features described above, as well as by its overall smaller size (see table 3).

REMARKS: The diagnosis given in the original description by Andersen (1910) still remains essentially valid. The large oval palatal fenestrations, commented on by Smith and Hood (1983), occur occasionally in this species but seem to be independent of age or sex. *Nyctimene cyclotis* ranges from sea level to near 1500 m and it has been collected sympatrically with *N. certans* at four localities between 780 and 1400 m.

SPECIMENS EXAMINED (with locality records for fig. 6): WEST IRIAN: **1.** Arfak Mt., 1°14'S,

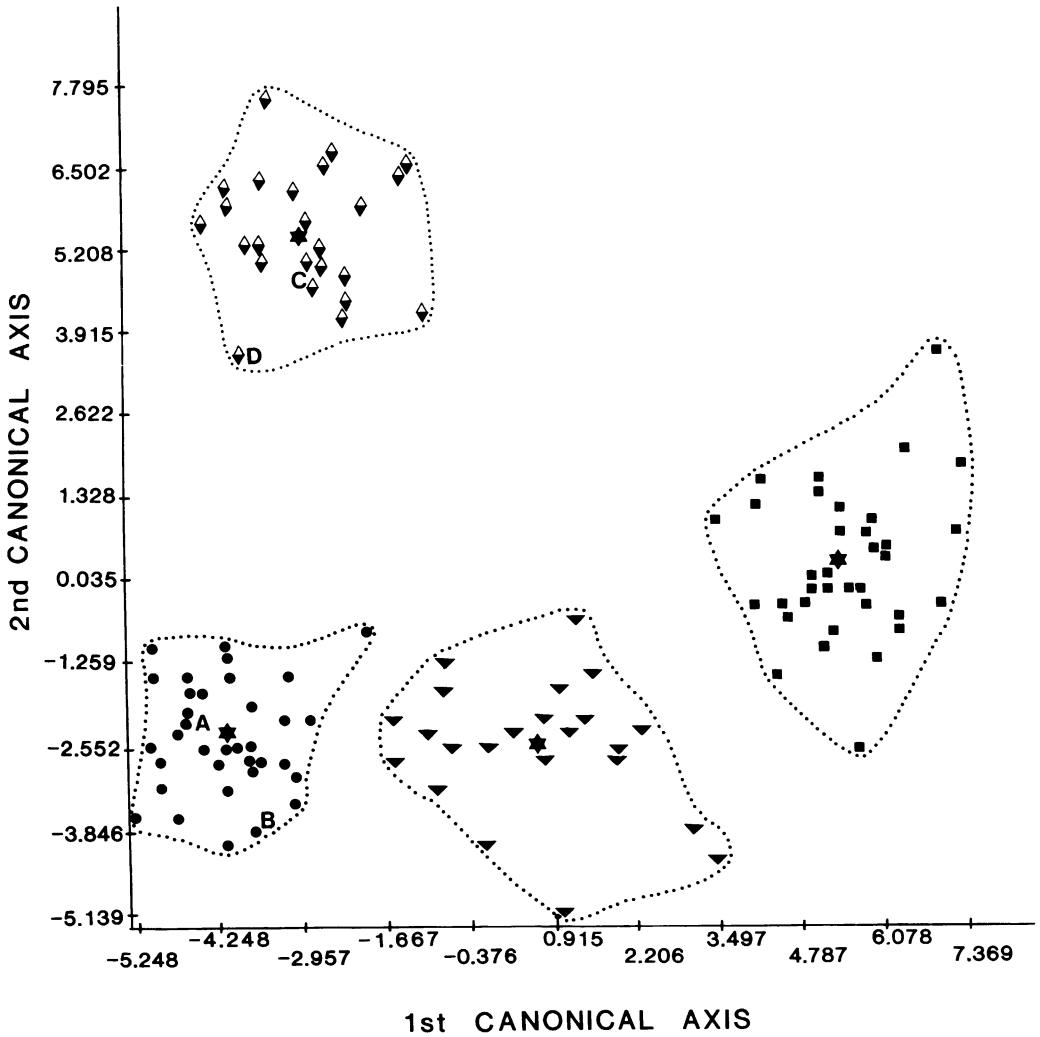

Fig. 5. Plot of individuals of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes* on the first and second canonical axes. Dots, *N. papuanus*; triangles, *N. cyclotis*; squares, *N. certans*; diamonds, *N. cephalotes*; stars, centroids for each group; A, holotype of *N. papuanus*; B, holotype of *N. a. minor*; C, D, topotypes of *N. cephalotes.*

134°01′E: BM(NH) 10.7.16.9 [holotype]. **2.** Ilaga Valley, Nassua Range, ca. 4°12′S, 147°26′E: AMNH 160347. PAPUA: **3.** Fly River, 5 mi below Palmer Junction, 5°56′S, 141°30′E, 80 m: AMNH 105091. **4.** West Sepik, Mt. Somoro, 3°25′S, 142°05′E, 1219 m: BBM-NG 101804. **5.** Morobe, Kalalo, 6°04′S, 147°11′E, 750 m: BBM-NG 52940 and 53143. **6.** Morobe, 10 km W Bulolo, 7°11′S, 146°34′E, 750 m: BBM-NG 51298, 51325, 51326 subadult, 51350, 51352, 51380, 53968, 54092, 54116 and 54129 subadults, 54234, and 54328. **7.** Morobe, Mt. Missim, south slope, 7°13′S, 146°43′E, 1350 m: BBM-NG 21059 (incomplete), 28396, 28410, and 53232–53234. **8.** Morobe, Mt. Missim, 7°13′S, 146°50′E, 1300 m: BBM-NG 24638 subadult. **9.** Morobe, Big Wau Creek Ridge, 7°19′S, 146°44′E, 1400 m: BBM-NG 29062 subadult. **10.** Owen Stanley Range, Efogi, 9°09′S, 147°37′E, 1408 m: CSIRO CM12593 and CM12594 subadult. **11.** Central Dist., Java Rarre, 9°25′S, 147°26′E, 600 m: BBM-NG 60287. **12.** Astrolabe Range, behind Baroka, 9°33′S, 147°26′E, 704 m: CSIRO CM12591, and 739 m: CM12592. **13.** Milne

TABLE 6
Canonical Analysis of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes*

Roots	*R*	R^2	Eigenvalue	Chi squared	df	χ^2 prob.	% trace	Cum. %
1	0.971	0.943	16.429	596.799	69	0.0000	62.67	62.67
2	0.950	0.903	9.270	292.408	44	0.0000	35.36	98.03
3	0.584	0.341	0.516	44.341	21	0.0025	1.97	100.00

Bay, Sinafade, 10°22'S, 150°30'E, 10 m: BBM-NG 24539. NEW BRITAIN: **14.** East New Britain, Warangoi, ca. 4°15'S, 152°00'E, 1584 m: BBM-NG 20914 (incomplete). **15.** East New Britain, Mt. Sinewet, 4°38'S, 151°59'E: BBM-NG 20757 subadult (incomplete).

Nyctimene certans Andersen, 1912a

Nyctimene certans Andersen, 1912a: 95.
Nyctimene cyclotis certans Laurie and Hill, 1954.

HOLOTYPE: Young adult [subadult?] unsexed skin and skull, BM(NH) 11.11.29.1, collected 20 January 1911 by A. S. Meek from Mount Goliath, West Irian. Skull badly damaged.

MEASUREMENTS OF HOLOTYPE: Length of tibia, 24.5; length of forearm, 58.0; lengths of metacarpals: second digit, 28.7; third digit, 38.4; fourth digit, 36.6; fifth digit, 37.4; lengths of first phalanges: third digit, 32.0; fourth digit, 24.4; fifth digit, 21.0; length of palate, 13.7; width across upper molars, 9.0; canine–molar length, 9.8; width across upper canines, 6.5; condyloincisive length of mandible, 22.8; lower canine–molar length, 11.2; width across lower third premolars, 7.4; height of coronoid process, 11.0.

DISTRIBUTION: West Irian and mainland Papua (see fig. 7 and "Specimens Examined" below).

COMPARISONS: See under comparisons of *N. cyclotis,* and tables 2, 3, and 4. In comparison with *N. cyclotis,* the skull of *Nyctimene certans* is longer (CBL 28.5–31.0) and relatively narrower, and its dorsal profile has a relatively longer, less elevated (flatter) nasal profile and a more elongate, less steeply arched braincase (see fig. 3).

Compared with *N. papuanus, N. certans* is much larger overall and differs markedly in its pelage, ears, and dentition.

Compared with *N. cephalotes,* the wings of *N. certans* have shorter forearms and metacarpals, but longer first phalanges. *N. certans* has similar lengths of skull and mandible, but differs from *N. cephalotes* significantly in all other cranial characters measured, as well as in its distinctive ears, pelage, and dentition (see tables 4, 5).

REMARKS: The age of the holotype of *N. certans* is somewhat problematical. Andersen (1912a) described it as an adult. Its metacarpals are shorter than those of any adults measured by me and are even shorter than those of the four subadults listed in table 2. Measurements of the first phalanges of digits

TABLE 7
Percentage of the Variance of Each Variable in Each Canonical Axis for *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes*

Variable	1st axis	2nd axis
FA	14.869	81.625
D2M	45.754	54.135
D3M	21.887	49.681
D31P	94.480	0.003
D4M	81.191	14.709
D41P	33.096	61.888
D5M	99.184	0.618
D51P	94.154	4.455
GL	68.862	31.117
CBL	0.780	95.259
PALL	87.826	7.319
ZYGO	99.975	0.025
MAST	51.734	18.898
BBC	0.000	88.714
HBC	5.126	94.874
M1M1	89.312	2.480
P3P3	82.433	16.893
C–M1	61.668	20.872
CCU	14.400	67.210
GLM	82.479	6.045
CM2L	47.092	52.762
P3P3L	43.217	55.649
HTCP	36.655	63.193

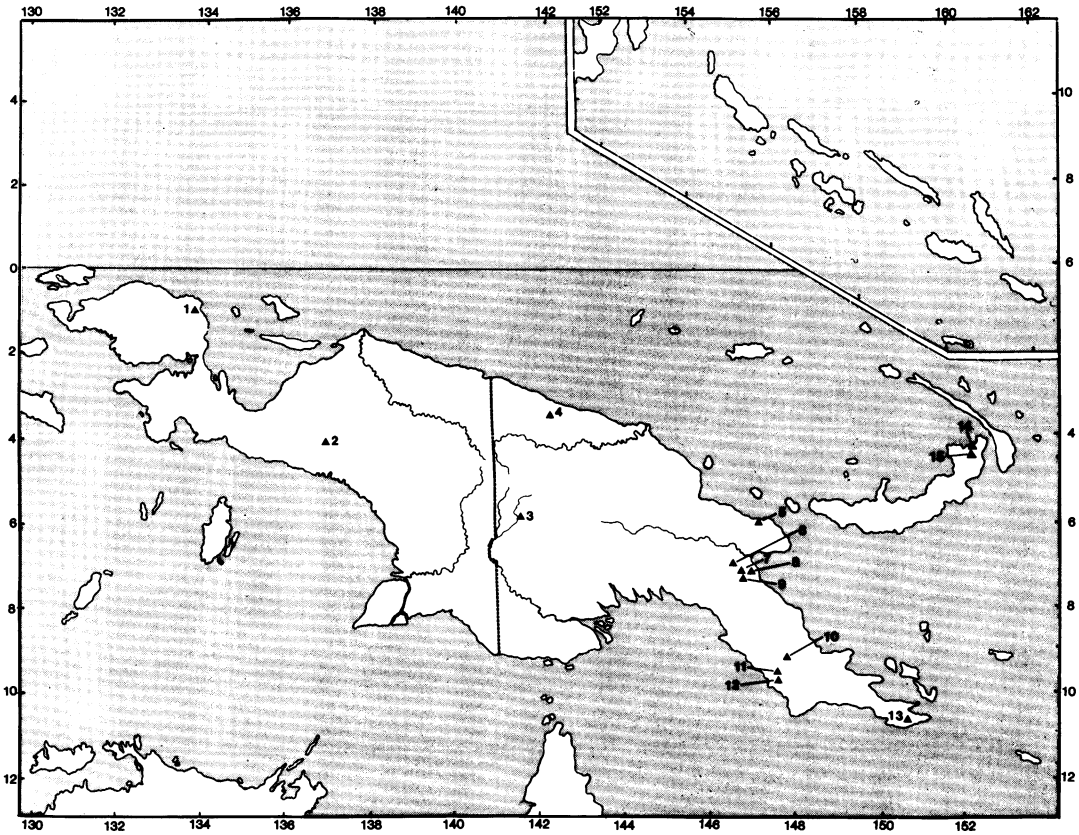

Fig. 6. Map of New Guinea and New Britain Islands with locality records for *Nyctimene cyclotis*. See "Specimens Examined" of this species for numbered localities.

three to five are all consistent with those of the subadults. The available cranial measurements are consistent with those of adults. The length of the mandible exceeds that of any specimen of *N. cyclotis* measured to date. Palatal fenestrations also occur occasionally in this taxon, but the observed examples were much smaller than those in *N. cyclotis*.

This species appears to favor higher elevations. One specimen was taken at 780 m and one at 1220 m, but all others occurred at 1340 m or higher.

SPECIMENS EXAMINED (with locality records for fig. 7): WEST IRIAN: **1.** Mount Goliath, 4°40′S, 139°52′E, ca. 3000 m: BM(NH) 11.11.29.1 [holotype]. PAPUA: **2.** Eastern Highlands, Kassam Pass, 6°18′S, 145°52′E, 1400 m: BBM-NG 54997–54998, 55001, 55021, and 55027. **3.** Bismarck Range, Aiyura, 6°20′S, 145°54′E, 2112 m: ROM 94059. **4.** Morobe, Mt. Shungol, 6°51′S, 146°44′E, 2000 m: BBM-NG 98283 and 98284. **5.** Morobe, 10 km W Bulolo, 7°11′S, 146°34′E, 780 m: BBM-NG 51300. **6.** Morobe, Mt. Missim, south slope, 7°13′S, 146°50′E, 1350 m: BBM-NG 28397 subadult, 28398, and 28404. **7.** Morobe, Mt. Forest, Coviak, 7°18′S, 146°43′E, 1319 m: BBM-NG 28467 and 28468. **8.** Morobe, Nakata Ridge, 7°20′S, 146°43′E, 1524 m: BBM-NG 28502. **9.** Morobe, Mt. Kiandi, 7°21′S, 146°43′E, 2060 m: BBM-NG 28448. **10.** Morobe, Big Wau Creek, 5 km SE Wau, 7°22′S, 146°43′E, 1400 m: BBM-NG 24589, 24600, 23613, 50598–50599, and 50689. **11.** Morobe, Bulldog Road, 7°28′S, 146°40′E, 2625 m: BBM-NG 28948 and 28959. **12.** Morobe, Bulldog Road, 12 mi from Edie Creek, 7°31′S, 146°40′E, 2405 m: BBM-NG 52452 and 54911. **13.** Owen Stanley Range, Efogi, 9°09′S, 147°37′E, 1408 m: CSIRO CM12595–12596, CM12597 subadult, and CM12598–12599, 1338 m:

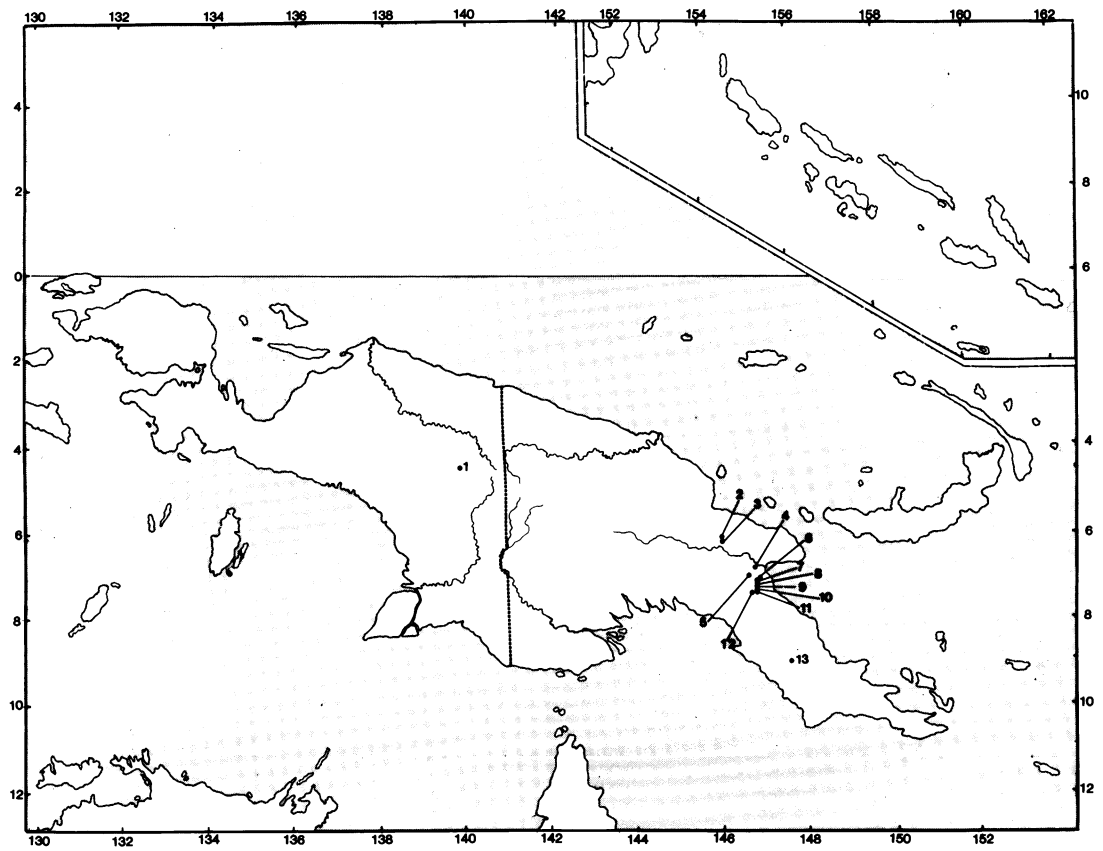

Fig. 7. Map of New Guinea and New Britain Islands with locality records for *Nyctimene certans*. See "Specimens Examined" of this species for numbered localities.

CM12600–12603, CM12604 subadult, CM12605–12606, CM12607 subadult, and CM12608.

Additional Specimens Examined

Nyctimene cephalotes (Pallas, 1767)

INDONESIA: Ambon: RMNH, 2 and one subadult. Sulawesi: Peleng Island; AMNH, 13. Toli Toli: USNM, 9.

Nyctimene papuanus Andersen, 1910.

WEST IRIAN: Oransbari: BBM-NG, 1. PAPUA: Fly River, 5 mi below Palmer Junction: AMNH, 3. Milne Bay: BM(NH), 1 [holotype]; Sinafade: BBM-NG, 3. Morobe Dist.: 10 km W Bulolo, BBM-NG, 5; Kalalo, BBM-NG, 1; Bupu R., 12 mi NE Lae, BBM-NG, 1; Singavwa R., near Lae, BBM-NG, 2; Sumsum, 20 km N Bulolo, BBM-NG, 1. Northern Dist.: Azarita, near Popondetta, BBM-NG, 1; Ambogosa R., near Popondetta, BBM-NG, 1; Popondetta, BBM-NG, 4; Soputa R., near Popondetta, BBM-NG, 1. Port Moresby area: Karema, Brown R. Forestry Sta., 38 km NW Port Moresby, BBM-NG, 2; Sogori, Siviuma Dam, BBM-NG, 2. SOLOMON ISLANDS: Bougainville Sound, AUM, 1; Bougainville Is., AUM, 1, and BBM-NG, 3; Kolombangara Is., BBM-NG, 1; Choiseul Is., BBM-NG, 1 [holotype *N. a. minor*]; Santa Ysabel Is., BBM-NG, 1.

SUMMARY

The taxonomic status of *Nyctimene cyclotis* and its relative, *N. certans* was studied in order to clarify their relationship. Comparisons with *Nyctimene cephalotes* and *N. papuanus* were made. *N. cyclotis* occurs on

mainland New Guinea (West Irian and Papua) and New Britain Islands, while *N. certans* is found on mainland New Guinea.

Although *N. cyclotis* and *N. certans* share dental, ear shape, and pelage characteristics, and occur sympatrically, there are sufficient differences for them to be considered distinct species. *N. cyclotis* and *N. certans* differed significantly from each other in 22 of 23 variables. There was no overlap in the condylobasal length of skull (CBL) between them. *N. cyclotis* averaged slightly smaller than *N. certans* for all variables analyzed for this study. *N. certans,* in comparison with *N. cyclotis,* has a longer, narrower skull, a flatter nasal profile, and a less steeply arched braincase.

In comparison with *N. papuanus, N. cyclotis* differs in dental features and has longer fur and broader ears. These latter features, as well as its overall smaller size, distinguish *N. cyclotis* from *N. cephalotes. N. certans* is larger overall than *N. papuanus* and differs markedly in its pelage, ears, and dentition. Compared with *N. cephalotes, N. certans* has shorter forearms and metacarpals but longer first phalanges. It also differs from *N. cephalotes* in cranial characters, ears, pelage, and dentition. Seven of 23 variables studied had significantly different means for all four species.

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Examination of Monophyly of Bats: Restriction Map of the Ribosomal DNA Cistron

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ABSTRACT

Two opposing hypotheses concerning the origin of bats, as well as flight in mammals, have been proposed. In one, all bats shared a common ancestor after diverging from the remainder of extant Mammalia, whereas in the other, Megachiroptera, Primates, and Dermoptera shared a common ancestor after diverging from the Microchiroptera. In the latter hypothesis, flight in mammals would have evolved twice. To discriminate between the two competing hypotheses, we mapped 52 restriction sites for the ribosomal cistron (rDNA) for representative taxa using a mole, a shrew, and *Mus* as outgroups. We examined 14 genera representing 13 families of Microchiroptera, 5 genera of Megachiroptera, *Cynocephalus* (order Dermoptera), and *Homo* and *Lemur* (order Primates). Of the 52 mapped restriction sites, 24 were shared among all taxa. Resolution of the two alternative hypotheses was not found within these data. The only potentially resolving site was a *Pvu* II site in the nontranscribed spacer that united Dermoptera with the five genera of Megachiroptera. No synapomorphic site linked all bats, all Microchiroptera, or Megachiroptera, Dermoptera, and Primates. It is hypothesized that the lack of resolution from these molecular data originates from these taxa sharing a common ancestor for a relatively short time after diverging from the remainder of extant Mammalia. Such a short time in a common ancestor would permit few molecular events in conservatively evolving DNA sequences to become established to document a common origin. Alternatively, events that became established in rapidly evolving molecules would be lost or obscured due to extensive evolution over the long term since the Primates, Megachiroptera, Microchiroptera, and Dermoptera separated from each other.

INTRODUCTION

Systematics is "the study of organismic diversity as that diversity is relevant to some specified kind of relationship thought to exist among populations, species, or higher taxa" (Wiley, 1981). Although this definition may be considered too narrow by some systematists, most would agree that one of the more important exercises in systematics is determining the phylogenetic relationships among taxa prior to any formal taxonomic treatment of those taxa. One of the most difficult tasks in systematics is the discovery of attributes or taxonomic characters that can be used to diagnose relationships. As Mayr (1982) stated, "the most frequent complaint made by a taxonomist is that the group of animals or plants on which he is working does not supply sufficient characters to allow an unequivocal decision on relationship." Therefore, systematists use a broad array of taxonomic char-

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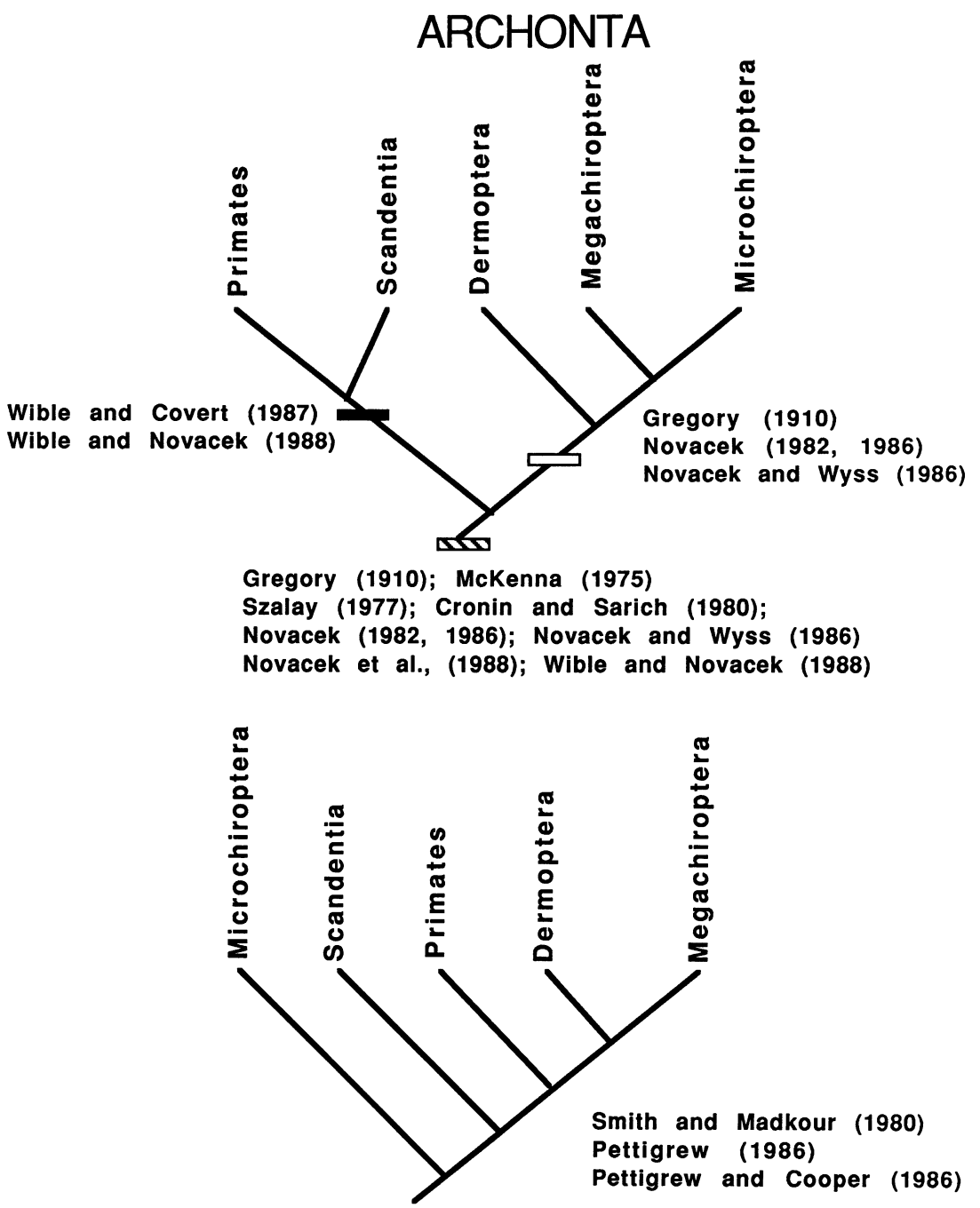

Fig. 1. Phylogenetic hypotheses depicting interordinal relationships in the Archonta. **Above.** Classical hypothesis. **Below.** Pettigrew hypothesis. References for studies supporting particular monophyly within the respective trees of both Archonta and groups within Archonta accompany the cladograms.

acters, including anatomy, histology, behavior, immunology, chromosomes, proteins, and DNA in an effort to resolve phylogenetic relationships and produce a classification.

The order Chiroptera represents a group of mammals that has received extensive attention from systematists for over 100 years, and many problems associated with both the phylogeny and classification of bats still exist. For instance, the New World bat family Phyllostomidae has been intensely studied using many different taxonomic characters, yet a number of questions pertaining to the recognition of monophyletic groups and the classification of phyllostomids persist (Baker et al., 1989). Even more troubling is the question of whether or not the order Chiroptera is a monophyletic group. Classically, the bats have been classified within a single taxon to the exclusion of other mammals (Linnaeus, 1758)—as monophyletic (Linnaeus, 1758)—but several recent authors have suggested that the order is diphyletic (fig. 1; Smith and Madkour, 1980; Pettigrew and Cooper, 1986).

The purposes of this study are twofold. First, a summary of opposing views and existing data that directly pertain to the question of chiropteran monophyly will be addressed. Second, empirical data will be provided for a detailed analysis of ribosomal DNA (rDNA) variation in chiropterans and related orders in an effort to stimulate more molecular systematics research on the chiropteran monophyly question.

CHIROPTERAN MONOPHYLY: Gregory (1910) recognized the superorder Archonta—containing the orders Chiroptera, Dermoptera, Scandentia, and Primates—and this clade was maintained in McKenna's (1975) classification. Although there have been criticisms of this grouping (Cartmill and MacPhee, 1980), several morphological studies and at least one immunological study (Cronin and Sarich, 1980) support the monophyly of this group. Nevertheless, some molecular studies place primates closer to other orders of mammals, including Lagomorpha and Rodentia (Schwale et al., 1984; De Jong, 1985; Miyamoto and Goodman, 1986). The associations among orders within Archonta are less clear (Novacek et al., 1988). Several authors, using erectile tissue of the penis (Smith and Madkour, 1980) and visual pathways of the central nervous system (Pettigrew, 1986; Pettigrew and Cooper, 1986; Pettigrew et al., 1989), have suggested that the order Chiroptera is diphyletic (fig. 1), with derived features that are shared between the suborder Megachiroptera and the orders Primates and Dermoptera being absent in Microchiroptera. This arrangement suggests that the mechanism for powered flight in bats, once considered the major feature uniting the two suborders, has been derived independently in the two groups. To the contrary, cranial and postcranial features suggest chiropterans to be monophyletic (fig. 1; Wible and Novacek, 1988). One additional study that disagrees with both the diphyly hypothesis of Pettigrew (1986) and the monophyly of Archonta involved a comparison of mitochondrial DNA nucleotide sequences of the cytochrome III gene (Bennet et al., 1988). The results of this study are unclear, because a true test for chiropteran monophyly was not performed. For instance, one bat genus (*Pteropus,* a megachiropteran) was compared to three mammalian orders: Primates, Artiodactyla, and Rodentia. *Drosophila* was used as an outgroup.

RIBOSOMAL DNA AS A TAXONOMIC CHARACTER: Our study was designed to determine if a cladistic analysis of restriction site data in the ribosomal DNA cistron could provide resolution of these systematic problems. With the recent advances in molecular biology, a plethora of potential systematic probes has been made available to molecular systematists for use in elucidating phylogenetic relationships. However, because the field of molecular systematics is relatively new, it is still unclear which molecules will provide adequate resolution to address a particular systematic question. Previous systematic studies using the ribosomal DNA gene complex have provided valuable information for addressing phylogenetic relationships (Gerbi, 1985; Appels and Honeycutt, 1986; Hillis and Davis, 1986, 1987; Suzuki et al., 1986; Dallas et al., 1988; Seperack et al., 1988; Mindell and Honeycutt, 1989; Van Den Bussche, 1989).

The rDNA gene complex is a tandemly repeated gene family consisting of coding and noncoding sequences that evolve at different rates. Coding regions (18S, 5.8S, 28S rDNA

genes) tend to be conserved across higher taxonomic levels (Elwood et al., 1985; Appels and Honeycutt, 1986). The internally transcribed spacer regions (ITS-1, ITS-2) that separate the coding regions, and the externally transcribed spacer regions (ETS) located at the 5'-end of the 18S rRNA gene, appear to be under fewer selective constraints than the coding regions and, hence, have been found to contain phylogenetically informative characters in many vertebrate groups (Wilson et al., 1984; Hillis and Davis, 1986, 1987; Mindell and Honeycutt, 1989; Van Den Bussche, 1989). Finally, separating the tandemly arranged coding regions is the most variable region, the nontranscribed spacer region (NTS). Subspecific, populational, and interindividual differences have been found for some taxa in this region (Davis, 1986; Suzuki et al., 1986; Suzuki et al., 1987; Dallas et al., 1988). Therefore, results from previous studies suggest that the rDNA complex should contain sufficient restriction site variability, either in the coding regions or in the transcribed spacer regions, to allow assessment of the higher phylogenetic relationships among the Chiroptera.

Materials and Methods

High-molecular-weight DNA was isolated from heart, kidney, liver, muscle, and/or placenta from the taxa listed in table 1, essentially following the method of Bingham et al. (1981). Genomic DNA was subjected to single and double digestion involving 18 different restriction endonucleases (*Bam*H I, *Bcl* I, *Bgl* II, *Bst*E II, *Cla* I, *Dra* I, *Eco*R I, *Hin*c II, *Hin*d III, *Kpn* I, *Nco* I, *Pst* I, *Pvu* II, *Sal* I, *Sst* I, *Stu* I, *Xba* I, *Xho* I). These 18 restriction endonucleases recognized a total of 108 nucleotides; 55 of these were either cytosine or guanine (50.9%). Therefore, the choice of enzymes was not significantly biased by either A:T- or G:C-rich recognition sequences. Digestion was accomplished with 2–4 units of enzyme per microgram of DNA for 3–12 hours under temperature and buffering conditions specified by the manufacturer. Digested fragments were separated on 0.6–2.0% agarose TAE (0.4 M Tris, 0.1 M Na_2EDTA, 0.05 M sodium acetate) gels with ethidium bromide and run at 30 mAmp for approximately 14 hours. Higher percentage agarose gels were used to improve resolution of the smaller fragments.

Separated DNA fragments were denatured in the gel by soaking in transfer solution (0.6 M NaCl, 0.4 M NaOH) for 30 minutes, and the denatured DNA was transferred to nylon hybridization membrane (Gene Screen Plus; DuPont) according to the techniques of Southern (1975), with modifications for alkaline transfer (Chomczynski and Qasba, 1984). Membranes were then washed in neutralizing solution (1.0 M Tris, 0.5 M NaCl; pH = 7.0) and allowed to air dry. Prior to hybridization with radioactive probes, the membranes were washed in prehybridization solution (1% sodium dodecyl sulfate [SDS], 50% formamide, 5% Denhardt's solution, 1.5% denatured salmon sperm DNA) at 37°C for 2–4 hours. All gels contained two internal size standards: Lambda DNA digested with *Hin*d III and a 1-kilobase (kb) ladder. Additionally, all mapping gels contained a lane with a sample of human DNA. This sample of human DNA served as a control to ensure that digestion had gone to completion, as well as to verify any site changes from the human sequence for this gene complex.

rDNA fragments were detected by hybridization with radioactively labeled rDNA clones of the 18S (p2546) and 28S (pI19) genes of *Mus musculus* (Arnheim, 1979). All rDNA probes were radiolabeled using the random priming method (Feinburg and Vogelstein, 1984). Labeled probes were denatured, combined with prehybridization solution (1×10^6 dpm/ml), and allowed to hybridize with the membranes for at least 12 hours at 37°C. After hybridization, the nylon membranes were washed (three times for 15 minutes at 42°C in 2× SSC, 0.1% SDS; twice for 30 minutes at 55°C in 0.1× SSC, 0.1% SDS) and exposed to X-ray film using two intensifying screens at −70°C (Laskey, 1979). Restriction endonuclease site maps for the transcribed portion of the rDNA were constructed using a combination of single and double digestion (Nathans and Smith, 1975). To increase accuracy in constructing restriction site maps, results from the human map were compared to the published sequence of the 18S (Torczynski et al., 1985), 5.8S (Nazar et al., 1976), and 28S (Gonzalez et al., 1985) rDNA genes.

Hypotheses of genealogy were based upon shared-derived characters—synapomorphies—as defined by Hennig (1966). Variable restriction sites, coded as present or absent, were used as phylogenetic characters, and trees were constructed using version 3.0 of PAUP (phylogenetic analysis using parsimony; developed by David Swofford). In addition, potential synapomorphies were also determined by a hands-on cladistic analysis using multiple outgroups, as suggested by Maddison et al. (1984) and Owen (1987). *Mus, Scalopus,* and *Crocidura* were used as outgroups in all phylogenetic analyses.

Specimens Examined

Order Rodentia

Mus musculus male (TK 28805): USA: Oklahoma, Cimarron Co., 3 mi E, 1.5 mi S Kenton.

Order Insectivora

Family Talpidae: *Scalopus aquaticus* male (29735): USA: Texas, Montgue Co., 3 mi N, 5 mi E Bowie.

Family Soricidae: *Crocidura* sp. (TK 21587): GABON: Estuaire Prov., Cap Esterias.

Order Primates

Family Hominidae: *Homo sapiens* male (TK 30732): USA: Texas, Lubbock Co., Lubbock, placenta donation from St. Mary's Hospital.

Family Lemuridae: *Lemur catta* male (TK 26899): USA: Texas, specimen from the Fort Worth Zoo; geographic origin unknown.

Order Dermoptera

Family Cynocephalidae: *Cynocephalus volans* male (TK 21407): THAILAND: Surat Thani Prov., Tha Chang Dist., 15 km N, 23 km W Ban Muruan.

Order Chiroptera

Suborder Megachiroptera

Family Pteropodidae: *Pteropus hypomelanus* female (TK 20225): PAPUA NEW GUINEA: East New Britain Prov., Duke of York Island, Rakauda Plantation. *P. macrotus* male (TK 20310): PAPUA NEW GUINEA: Central Prov., Lakoke Quarantine Station, 9 km NE Fort Moresby. *Rousettus* (TK 27199): KENYA: Western Providence, Kakamega District, 6 km S, 6 km W Kakamega. *Megaloglossus* sp. female (TK 21507): GABON: Estuaire Prov., Cap Esterias. *Megaloglossus* sp. female (TK 21566): GABON: Estuaire Prov., 2.5 km SE Cap Esterias. *Nyctimene* sp. female (TK 20095): NEW GUINEA: East New Britain Prov., Gela Gela Plantations. *Nyctimene* sp. male (TK 20096): NEW GUINEA: East New Britain Prov., Gela Gela Plantations. *Nyctimene* sp. male (TK 20101): NEW GUINEA: East New Britain Prov., Gela Gela Plantations.

Family Macroglossinae: *Macroglossus* sp. female (TK 20239): PAPUA NEW GUINEA: East New Britain Prov., Duke of York Islands, Rakauda Plantations. *Macroglossus* sp. male (TK 20306): PAPUA NEW GUINEA: Central Prov., Lakoke Quarantine Station, 9 km NE Fort Moresby. *M. sobrinus* female (TK 21445): THAILAND: Surat Thani Prov., Tha Chang Dist., 15 km N, 23 km W Ban Muruan.

Suborder Microchiroptera

Family Rhinopomatidae: *Rhinopoma microphyllum* female (TK 25611): JORDAN: Jordan Valley, Tabqat Fahl Ruins. *R. microphyllum* female (TK 25612): JORDAN: Jordan Valley, Tabqat Fahl Ruins. *Rhinopoma* sp. male (TK 25644): PALESTINE: West Bank of Jordan, Jericho, Mt. Quarantania. *Saccopteryx leptura* female (TK 19493): VENEZUELA: Barinas, 38 km SE Varinas on hwy 4.

Family Megadermatidae: *Megaderma lyra* female (TK 21288): THAILAND: Uthi Thani Prov., Lansak Dist., Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary Headquarters.

Family Nycteridae: *Nycteris graudis* male (TK 21558): GABON: Estuaire Prov., 2 km SE Cap Esterias. *N. graudis* female (TK 21559): GABON: Estuaire Prov., 2 km SE Cap Esterias.

Family Rhinolophidae: *Rhinolophus euryotis* male (TK 20037): NEW GUINEA: East New Britain Prov., 2 km S Gunanur.

Family Hipposideridae: *Hipposideros commersoni* female (TK 33178): KENYA: Coastal Prov., Kwale Dist., Shimba Hills National Reserve, Mwele Forest, 12 km S, 11 km W Kwale.

Family Phyllostomidae: *Macrotus californicus* male (TK 28985): USA: Arizona, Pinal Co., 27.0 mi SW Casa Grande, Old Mammon Mine. *M. waterhousii* female (TK 27727): JAMAICA: St. Ann's Parish, Green Grotto Cave, 23 km SW St. Ann's Bay.

Family Mormoopidae: *Mormoops megalophylla* male (TK 19312): VENEZUELA: Barinas, 7 km NW Barinitas.

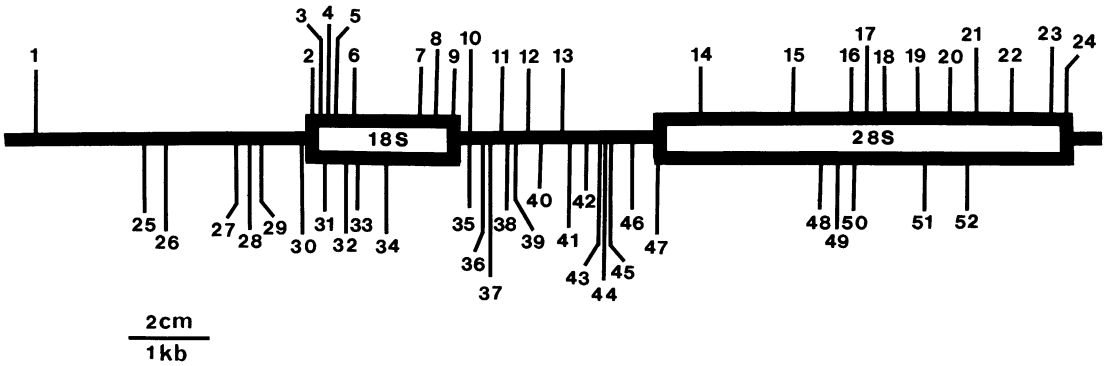

Fig. 2. Restriction endonuclease site map of the transcribed portion of the rDNA gene complex showing conserved sites on top and variable sites below. Sites are numbered as follows: *Bam*H I 15, 19, 25, 32, 335, 42; *Bcl* I 13; *Bgl* III 17; *Bst*E II 4, 7, 40, 46, 50, 52; *Cla* I 1, 33; *Dra* I 5m, 12m, 49; *Eco*R I 8, 23; *Hinc* II 14, 21, 29; *Hind* III 9; *Kpn* I 11; *Nco* I 3, 16, 24, 38; *Pst* I 6, 45, 51; *Pvu* II 20, 26, 41; *Sal* I 27, 36, 47; *Sst* I 18, 22, 31, 34, 43; *Stu* I 30, 37, 48; *Xba* I 2, 10; *Xho* I 28, 39, 44. The numbering of sites is the same as in table 1.

Family Noctilionidae: *Noctilio leporinus* female (TK 19129): VENEZUELA: Bolivar, 8 km S, 5 km E El Manteco. *Noctilio leporinus* male (TK 19077): VENEZUELA: Bolivar, 2.5 km E El Manteco.

Family Molossidae: *Tadarida brasiliensis* male (TK 21816): USA: North Carolina, Cumberland Co., Fayetteville.

Family Natalidae: *Natalus* sp. female (TK 15663): DOMINICA: St. John Co., 0.5 mi N Toucari. *Natalus* sp. male (TK 15665): DOMINICA: St. John Co., 0.5 mi N Toucari.

Family Thyropteridae: *Thyroptera* sp. (TK 19255): VENEZUELA: Bolivar, 8 km W El Manteco.

Family Furipteridae: *Furipterus horrens* female (TK 17149): SURINAME: Saramacca, Voltzbert.

Family Vespertilionidae: *Lasionycteris noctivagans* female (TK 24216): USA: Texas, Lubbock Co., Lubbock.

Acknowledgments

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RESULTS

The rDNA repeat of the 25 taxa examined was mapped using 18 restriction endonucleases. The overall repeat unit length in these taxa ranged between 38 and 43 kb, with most length variation mapping to the nontranscribed spacer. Few restriction sites in the NTS were conserved among species, and the size of the NTS—in combination with length variation and probes restricted to the transcribed region of the rDNA repeat—limited the value of the NTS for detailed phylogenetic comparisons. Additional length variation (10–70 base pairs) was also found in the 28S gene region, but this variation was restricted to "divergent domains" or "expansion segments" known to vary in length among mammals and other vertebrates (Clark et al., 1984; Hassouna et al., 1984; Hillis and Davis, 1987).

Of the 52 mapped restriction sites, 24 sites were shared among all taxa (fig. 2; table 1). Most of the conserved sites were located within the coding regions (18S and 28S rRNA genes) and the internal transcribed spacer (ITS-1). Two restriction sites, *Hinc* II site 21 (*Homo, Megaderma,* and *Nycteris*) and *Sal* I site 47 (*Saccopteryx*), were polymorphic within individuals having two repeat types defined by the presence or absence of these sites (table 1). The 28 variable sites occurred primarily in the internal transcribed spacer,

TABLE 1

Restriction Endonuclease Site Map for the Ribosomal DNA Cistron for 25 Mammmalian Genera
(0 = absent; 1 = present; 2 = polymorphic. Position of each site is identified by character number in figure 1.)

	Enzyme (letter) and character number																								
	C 1	A 2	N 3	Z 4	D 5	T 6	Z 7	E 8	H 9	A 10	K 11	D 12	L 13	R 14	B 15	H 16	G 17	Q 18	B 19	P 20	R 21	Q 22	E 23	N 24	B 25
Mus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
Scalopus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Crocidura	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Homo	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lemur	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cynocephalus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pteropus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Rousettus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Megaloglossus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Nyctimene	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Macroglossus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Rhinopoma	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Saccopteryx	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Megaderma	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1
Nycteris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1
Rhinolophus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hipposideros	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Macrotus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mormoops	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Noctilio	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tadarida	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Natalus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Thyroptera	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Furipterus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lasionycteris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

the NTS upstream of the 18S gene, and the 5′-end of the 28S gene. Twelve of these 28 sites have been lost or gained in only one species (autapomorphic for single taxon) and are therefore phylogenetically uninformative.

The remaining 17 variable sites were used to evaluate the alternative phylogenetic hypotheses of chiropteran monophyly versus diphyly. Of these sites, six occur in the NTS and externally transcribed spacer, one in 18S genes, eight in the ITS, and two in the 28S gene. Each of these 17 variable sites was treated as a character and scored as present or absent, and the character matrix (table 1) was used in a parsimony analysis employing version 3.0 of PAUP. Two approaches were used in this analysis, and in each case *Mus* and the insectivores (*Scalopus* and *Crocidura*) were used as outgroups. First, existing phylogenetic hypotheses for relationships among orders in Archonta were tested with the assumption that each chiropteran suborder represented a monophyletic group, with relationships among taxa within suborders based on those proposed by Smith (1976) for Microchiroptera and Haiduk (1983) for Megachiroptera. Second, the data set was analyzed heuristically using global branch-swapping (MULPARS option) in PAUP. As can be seen in figure 3 (a and b), the monophyly and diphyly hypotheses have tree lengths of 46 and 45, respectively. The level of ambiguity in both of these trees can be seen by the low consistency index (CI = 0.348 for fig. 3a and 0.356 for fig. 3b), thus revealing high levels of homoplasy. Several clades are supported by synapomorphies: (1) monophyly of Megachiroptera (3 characters); (2) sister-group relationship of *Mormoops* and *Noctilio* (3 characters); (3) monophyly of Phyllostomatoidea (*Macrotus, Noctilio,* and

TABLE 1—(*Continued*)

Enzyme (letter) and character number																									
P	S	X	R	U	Q	B	C	Q	B	S	U	N	X	Z	P	B	Q	X	T	Z	S	U	D	Z	T	Z
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0
1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	1	0	1	0
1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1
0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0
0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0

Mormoops) (1 character); (4) monophyly of microchiropteran families Hipposideridae, Rhinolophidae, Megadermatidae, Nycteridae, Emballonuridae, and Rhinopomatidae (1 character); and (5) sister-group relationship between order Dermoptera (*Cynocephalus*) and Megachiroptera in figure 3b (1 character). Unfortunately, most synapomorphies characterizing particular clades are homoplastic (have low consistency indices), with the exception of three characters in figure 3a and four characters in figure 3b that have consistency indices of 1.00. One of these characters defines the dermopteran/megachiropteran clade, thus making the order Chiroptera diphyletic. Because this character is not shared by *Homo* or *Cynocephalus,* there is no support for a Primates/Dermoptera/Megachiroptera association.

A heuristic search restricted to the first 100 trees followed by the construction of a strict consensus tree yielded a tree of length 43. In this analysis, megachiropteran monophyly was supported, as well as a clade uniting *Mormoops* and *Noctilio.* The only other clade was one depicting the associations of *Homo* and *Rhinolophus* (a microchiropteran bat) and *Pteropus/Megaloglossus* (different megachiropteran subfamilies). All other relationships were unresolved.

DISCUSSION

Examination of figure 3 reveals how few synapomorphies document clades in the alternative trees. The only clades supported by synapomorphies that do not involve homoplastic events are the common ancestry of the five genera of Megachiroptera (character 25), the common ancestry of the Megachiroptera and Dermoptera (character 26) to the exclusion of all other taxa examined, and the

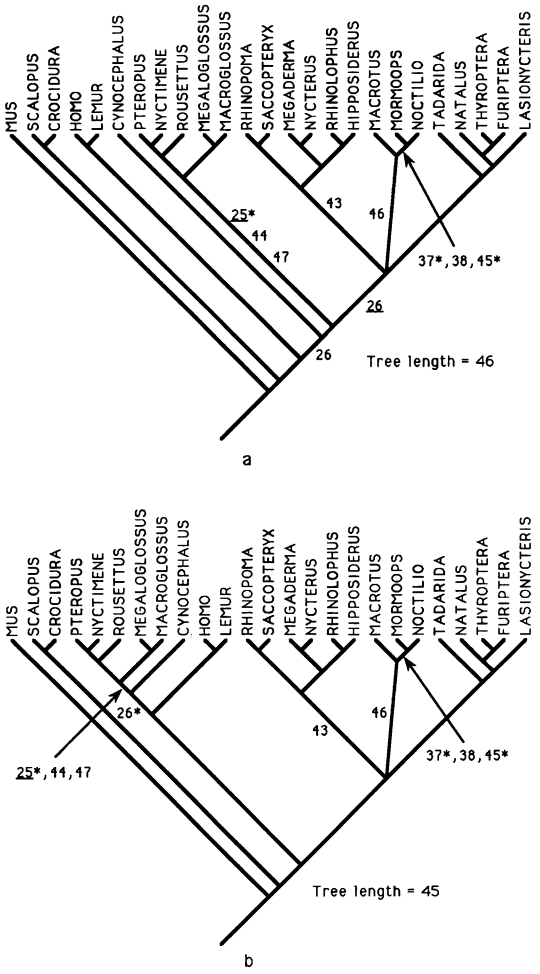

Fig. 3. **a.** Apportionment of characters along branches defining a tree that supports chiropteran monophyly—classical hypothesis. **b.** Characters supporting chiropteran diphyly—Pettigrew hypothesis. The tree lengths and assignment of characters throughout the tree were established by (PAUP) phylogenetic analysis using parsimony. Asterisk (*) identifies characters with a consistency index of 1.00. All other characters have CIs lower than 1.00. Underlined characters are site losses and those with no underline are site gains.

common ancestry of *Mormoops* and *Noctilio* (table 1; fig. 3). We do not conclude that the difference between 46 steps required for the classical hypothesis (fig. 3a) and 45 steps required for the Pettigrew hypothesis (fig. 3b) is significant. The rDNA data do not provide a synapomorphy that documents either the common ancestry of all bats (classical hypothesis) or a common ancestry between Primates and megachiropterans after divergence from the Microchiroptera (Pettigrew's hypothesis). Therefore, we conclude that this data set provides no clear resolution of the debate over the shared common ancestry of Dermoptera/Primates/Megachiroptera to the exclusion of the Microchiroptera.

The lack of resolution observed among these mammal groups is surprising considering the utility of the rDNA complex in addressing phylogenetic hypotheses associated with higher taxonomic categories of other vertebrate groups (Hillis and Davis, 1986; Mindell and Honeycutt, 1989). Just how serious is this lack of resolution? Is there any level of divergence among these 25 mammalian taxa where the rDNA molecule provides useful phylogenetic information? Unfortunately, the prognosis for the rDNA molecule providing information on mammal relationships is poor. For instance, the following well-established clades based on a variety of morphological studies and standard classifications were not supported by rDNA synapomorphies: (1) monophyly of prosimians (*Lemur*) and simians (*Homo*); (2) monophyly of insectivores (*Crocidura/Scalopus*); and (3) monophyly of the Rhinolophidae (*Rhinolophus/Hipposideros*). Collectively these results suggest that the "evolutionary window" provided by the rDNA restriction site data is narrow relative to resolving particular relationships among mammals and that even when synapomorphies are provided, the number of these characters supporting nodes will be small and the consistency of individual synapomorphies at nodes will be low. We therefore conclude that the rDNA molecule provides little insight into the mammalian origins and cladogenetic events leading to these 25 taxa.

What then do our data indicate? The only synapomorphy that may provide some information pertinent to the question of chiropteran monophyly is character 26, which unites *Cynocephalus* with the five megachiropteran genera. This character has a consistency of 1.00 and does depict a site gain as opposed to a site loss. If we accept character

26 as supporting a common ancestry for the Dermoptera and the suborder Megachiroptera, then the order Chiroptera (including Megachiroptera and Microchiroptera) is diphyletic and flight would by necessity have arisen twice or alternatively would have been lost in the Dermoptera. The question then becomes, "How much credibility can we give to character 26?" In light of the extreme inconsistency associated with other characters, we suggest that one should be cautious of overinterpreting single synapomorphies. The only other clade concordant with other character sets is the Phyllostomidae (*Macrotus, Noctilio,* and *Mormoops*), which was supported by one synapomorphy in this study. However, this character is homoplastic. Some examples (table 1) of the inconsistency in our data include character 27 (uniting *Homo, Pteropus, Megaloglossus,* and *Rhinolophus*), character 38 (uniting *Megaderma, Noctilio,* and *Mormoops*), character 40 (uniting *Megaderma, Natalus,* and *Thyroptera*), character 42 (uniting *Rousettus* and *Lasionycteris*), character 43 (uniting *Cynocephalus, Saccopteryx, Nycteris, Rhinolophus, Pteropus, Rousettus, Megaloglossus, Macroglossus, Nyctimene,* and *Macrotus*), and character 45 (uniting *Macrotus* and *Noctilio*).

Are there any other explanations for the lack of resolution provided by restriction site variation of the rDNA cistron relative to the relationships among bat families and other mammalian taxa? One possibility is that these taxa underwent a rapid radiation, having a short time frame of shared common ancestry during which synapomorphies could become established. If this is true, then other molecular studies of early bat evolution will likely encounter problems similar to those observed in this data set. Synapomorphies from any data set that document most ordinal-level relationships in mammals as well as familial-level relationships in bats are few. Perhaps systematic studies should be concerned not only with topologies, contents of clades, and levels of incongruence, but also with the actual internode lengths defining particular monophyletic groups. It could be that a combination of relatively short periods of shared common ancestry between diverging lineages and long periods of time subsequent to particular cladogenic events makes resolving branching patterns rather difficult regardless of the characters used to diagnose relationships. It is interesting that a study of 45 genera of phyllostomoid bats by Van Den Bussche (1989) found a greater amount of resolution and fewer obvious homoplastic events than the present study. However, his study also encountered extreme conservatism in the evolution of this gene complex. If the internode length explanation of the absence of synapomorphies is correct, then most well-established clades documented by rDNA synapomorphies (Van Den Bussche, 1989) can be expected to be supported by unrelated sets of characters.

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Morphometrics of the Family Emballonuridae

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ABSTRACT

Morphometric analysis revealed three distinctive groups among the genera of emballonurids. *Taphozous–Saccolaimus* is a group distinctive in size and shape, particularly cranially. Diclidurids are distinctive in appendicular characters only, especially those in the wing. The third group includes all other emballonurids. Phylogenetic studies also separated *Taphozous–Saccolaimus* as distinctive but included diclidurids among other New World species. Compared with molossids, emballonurids are morphometrically quite homogeneous.

INTRODUCTION

Miller (1907) thoroughly described most of the extant families of bats and illustrated several of the genera with exquisite line drawings. His work remains valuable for its clarity and for establishing a description of and qualitative differences among the morphologies of families and genera of Chiroptera.

We have been interested for some years in the quantitative morphological differences among genera within families and among families (Freeman, 1981; Lemen and Freeman, 1981, 1984). In this morphometric treatment of the family Emballonuridae, the sheath-tailed bats, we examine the quantitative differences among the species and genera within the family, compare the morphometric groupings with groupings from two phylogenetic studies, and describe the morphometric variation between the families Emballonuridae and Molossidae, the free-tailed bats.

Early generic treatments of emballonurids include Troughton's (1925) revision of the Australasian genera *Taphozous* and *Saccolaimus,* Sanborn's (1937) study of American species, and Tate and Archbold's (1939) examination of the genus *Emballonura.* More recently Barghoorn (1977) examined cranial morphology of a fossil genus, *Vespertiliavus,* and all Recent genera for their possible phylogenetic relationships, and Robbins and Sarich (1988) produced a phylogenetic study of the family using protein electrophoresis and immunology.

METHODS

Thirty-eight meristic characters (27 cranial and 11 appendicular) were studied on 37 species of emballonurid bats. These are standard measurements and, for the most part, a subset of those in Freeman (1981). There are some changes, however, because of structural differences between molossids and emballonurids. Because there is no comparable third phalanx and cartilaginous tip of digit III in emballonurids, the quantity measured for both families is the length from the second phalanx to the tip of that digit. Postorbital and interorbital breadths in some emballonurids had to be measured inferior to any supraorbital bone overhanging those breadths in order to measure the least constriction. This was particularly true with the diclidu-

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rids. The quantity SIZE equals the sum of the natural logs of greatest skull length (which differs slightly from condylocanine length; used in Freeman, 1984, 1988), zygomatic breadth, and height of braincase. SIZE correlates well with weight of the animal (Freeman, 1988).

Both bivariate and multivariate analyses were used to assess the data, including principal components analysis with and without a "shearing" function. The shear method described by Bookstein et al. (1985) is particularly useful in our analysis because it generates a size factor based on within-genus comparisons and not the first principal component of the entire data set, as used in "sizeout." The distinction between the sizeout approach and shearing is particularly important in this data set because the bats in the *Taphozous–Saccolaimus* group are much larger than the majority of Emballonuridae. The sizeout approach will tend to define shape differences between *Taphozous–Saccolaimus* and other bats as size-related differences. This would indicate that bats of the *Taphozous–Saccolaimus* group are not different in shape. Shearing does not use the size differences among groups in its definition of size, and in this case *Taphozous–Saccolaimus* is found to have considerable shape differences compared to other Emballonuridae (fig. 1). Finally, simple regression analyses were performed on each character versus the SIZE quantity.

We examined the following species for this study: a. *Balantiopterx io,* b. *Balantiopterx plicata,* c. *Centronycteris maximiliani,* d. *Coleura afra,* e. *Cormura brevirostris,* f. *Diclidurus albus,* g. *Diclidurus ingens,* h. *Diclidurus isabella,* i. *Diclidurus scutatus,* j. *Emballonura alecto,* k. *Emballonura atrata,* l. *Emballonura beccarii,* m. *Emballonura monticola,* n. *Emballonura nigrescens,* o. *Emballonura raffrayana,* p. *Emballonura semicaudata,* q. *Emballonura sulcata,* r. *Peropteryx leucoptera,* s. *Peropteryx kappleri,* t. *Peropteryx macrotis,* u. *Peropteryx trinitatis,* v. *Rhynchonycteris naso,* w. *Saccopteryx bilineata,* x. *Saccopteryx canescens,* y. *Saccopteryx leptura,* A. *Taphozous australis,* B. *Taphozous hamiltoni,* C. *Taphozous hildegardeae,* D. *Taphozous longimanus,* E. *Taphozous mauritianus,* F. *Taphozous melanopogon,* G. *Taphozous nudiventris,* H. *Taphozous perforatus,* I. *Taphozous theobaldi,* J. *Saccolaimus flaviventris,* K. *Saccolaimus peli,* and L. *Saccolaimus saccolaimus.*

The following measurements were taken (descriptions and illustrations are in Freeman, 1981): **Cranial:** greatest skull length, palatal length, maxillary toothrow, upper molariform row, lacrimal width, interorbital width, postorbital width (POSTORB), zygomatic breadth, breadth at mastoids, breadth of braincase, height of braincase, height of upper canine, length M3 (M3LENGTH), width M3, width at upper canines, width at upper molars, dentary length, dentary–condylocanine length, condyle to M3 length, lower toothrow, moment arm of temporal, moment arm of masseter, height of coronoid, dentary thickness, height of condyle above toothrow, height of lower canine, and length of condyle; **Appendicular:** tibia, forearm, third metacarpal, third metacarpal first phalanx (PHAL1M3), third metacarpal second phalanx to tip, fourth metacarpal, fourth metacarpal first phalanx, fourth metacarpal second phalanx, fifth metacarpal, fifth metacarpal first phalanx (PHAL1M5), and fifth metacarpal second phalanx.

Abbreviations used in the text include PC1, principal component one; PC2, principal component two; PC3, principal component three; H2, sheared component 2; and H3, sheared component 3.

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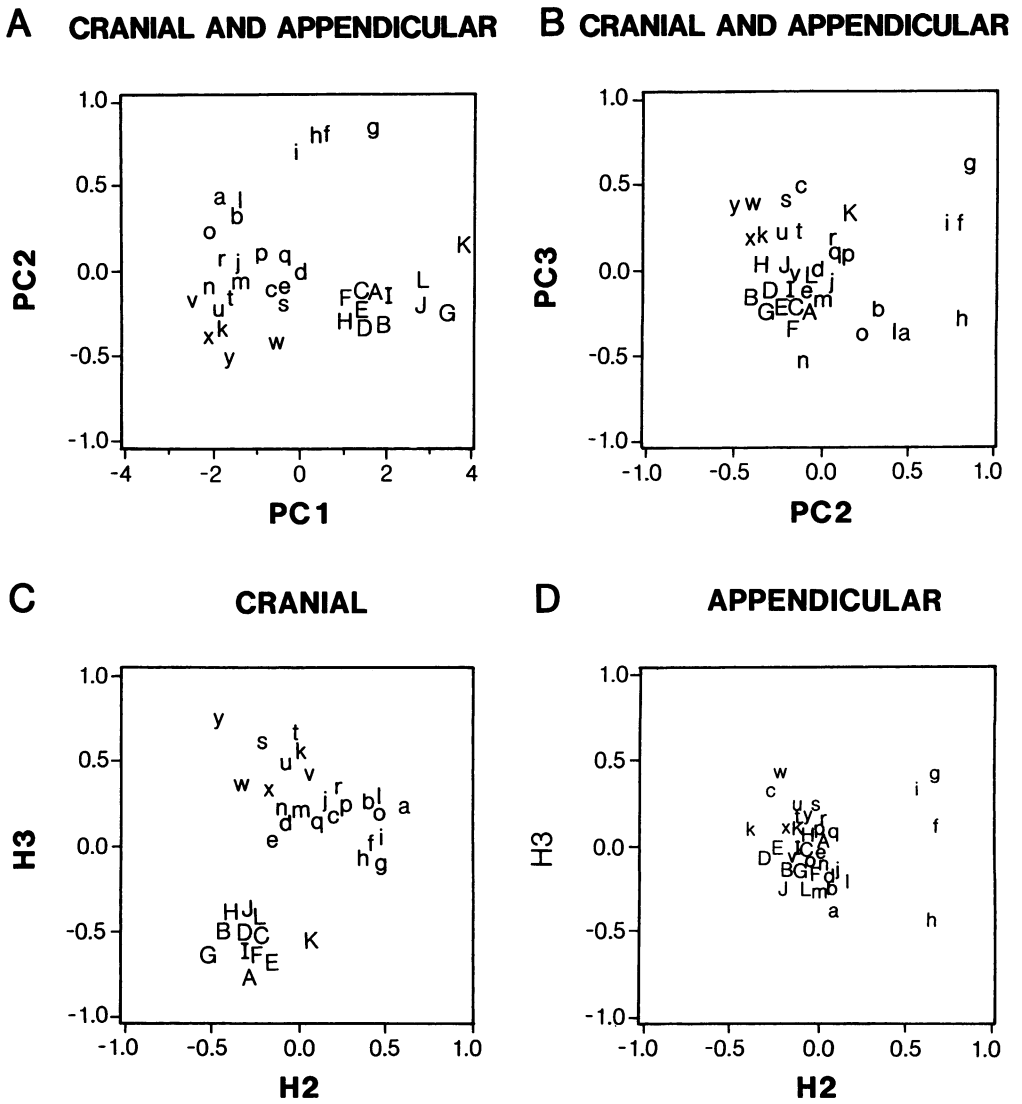

Fig. 1. The first three principal components of an analysis of the emballonurid data set with cranial and appendicular measurements (**A** and **B**). Separate analyses using sheared components were run on cranial measurements alone and on appendicular measurements alone (H2 and H3 in **C** and **D**). Species are indicated by letters, which are listed in Methods.

her mentors at the American Museum; for patiently wading through new methodology and giving excellent help as a member of her dissertation committee; for leaving characteristic, cryptic, and dependable notes on specimen tags of bats and other mammals in most of the major collections around the country, particularly at Field Museum; for being a colleague of encyclopedic knowledge who unselfishly shares that knowledge; and for being a continual source of stimulation and friendship.

RESULTS

Morphological trends in the data, revealed by principal components analysis, revolve around general size, several wing measure-

ments, width-of-face measurements, and a tooth measurement. Eighty-seven percent of the variation in the family can be explained by the first component, which is related to a change in size. Size typically explains most of the variation in morphological studies on quantitative characters and is typically the first principal component. Component two explains 3.5 percent of the variation and is influenced primarily by the length of the first phalanx of digit III (shortest at positive end), postorbital width (widest at positive end), length of first phalanx of digit V (longest on positive side), and interorbital width (widest at positive end). Component three explains 1.9 percent of the total variation and is influenced by length of second phalanx of digits IV and V (longest at positive end) and length of M3 (longest at positive end).

The placement of species on the first two components, shows species of *Taphozous–Saccolaimus* well separated from all other genera except *Diclidurus* because of their larger size (fig. 1A). *Diclidurus* is distinct from all other genera because of its wing configuration (unusually short first phalanx of digit III and long first phalanx of digit V), wide postorbital and interorbital breadths, and somewhat longer M3s. On PC3 *Diclidurus* is less cohesive because *Diclidurus isabella* has a short second phalanx of digit IV, and of digit V to a lesser degree, while the other three species in the genus have long ones (fig. 1B). All other emballonurid genera—*Emballonura, Coleura, Rhynchonycteris, Saccopteryx, Centronycteris, Peropteryx, Cormura,* and *Balantiopteryx*—are in one large indistinguishable group.

Using the shearing method to remove the effect of size gives somewhat different results. The main difference is that the *Taphozous–Saccolaimus* group forms a distinctive morphological entity based on cranial characters but not appendicular characters (fig. 1C). *Diclidurus* is highly distinctive based on features of the wing but much less so for cranial features (fig. 1D).

In examining the makeup of the multivariate analyses, we regressed each of the 38 characters against a composite quantity to represent size (see Methods). A sample of the characters that are heavily loaded on components two and three can be seen as extremes from the regression line to a greater or lesser degree in the bivariate plots (fig. 2). The simple plots clarify and verify the multivariate picture so that it is easy to see what characters influence the principal components.

DISCUSSION

Morphological relationships within the emballonurids parallel the phylogenetic hypotheses of Robbins and Sarich (1988) in some cases, and run contrary to them in others. The most basic split discovered by Robbins and Sarich was *Taphozous* and *Saccolaimus* versus the rest of the emballonurids. Our data show that *Taphozous* and *Saccolaimus* are a distinctive group in size and cranial shape. This is a case where time has increased morphological distinction between groups. The next most distinctive group is the genus *Diclidurus.* Its skull morphology is similar to that of *Balantiopterx,* and both occupy an extreme of H2 (fig. 1C). However, *Diclidurus* is distinct in wing morphology. The recognition of this genus as a separate subfamily is based largely on postcranial morphology, particularly the shape of the clavicle and the construction of the tibia, but also, because the cranium has a wide supraorbital bone that overhangs the interorbital/postorbital region (Miller, 1907; Koopman, 1984b). Electrophoretic data indicate that *Diclidurus* belongs within the large group of New World genera. If Robbins and Sarich (1988) are correct, this is a case where morphological distinctiveness does not indicate phylogenetic distance.

Another finding of Robbins and Sarich (1988) was recognition of the *Emballonura–Coleura* group of Old World bats versus the New World genera. This differs from Barghoorn's (1977) placement of *Coleura* with the New World forms. However, his placement of *Coleura* was based on the loss of an incisor. Tooth reduction may occur in unrelated taxa, reducing the reliability of this character. Overall, we prefer the grouping of Robbins and Sarich (1988). Actually, the electrophoretic data indicate that *Emballonura* is paraphyletic, with *Coleura* included within. Our

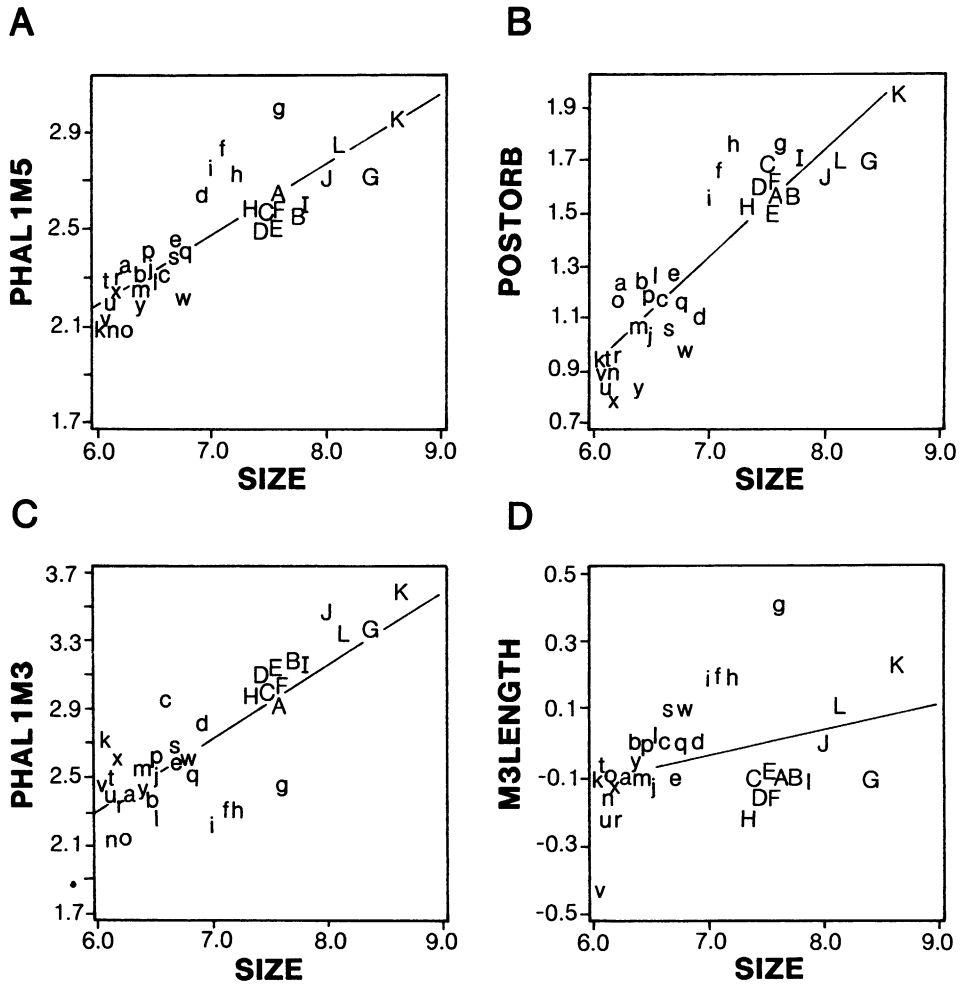

Fig. 2. Bivariate plots for variables (natural logs) first phalanx of digit III (**A**), postorbital breadth (**B**), first phalanx of digit V (**C**), and length of M3 (**D**) against SIZE (see Methods for explanation of SIZE). Lines plotted in each scattergram are linear regression lines; the relevant statistics for the lines are (**A**) a = 0.43, b = 0.29, $P < 0.0001$; (**B**) a = −1.52, b = 0.40, $P < 0.0001$; (**C**) a = −0.36, b = 0.44, $P < 0.0001$; and (**D**) a = −0.56, b = 0.07, $P < 0.03$. Species are indicated by letters, which are listed in Methods.

morphological data indicate a close similarity between *Emballonura* and *Coleura*. There is, however, no great distinction between these two genera and the New World forms.

Miller (1907: 85) stated under principal subdivisions in the family that "the genera of Emballonuridae as a whole form a very homogeneous group, but the South American *Diclidurus* is so different from the others that it must be regarded as forming a distinct subfamily." Simpson (1945: 55) lumped many of the New World genera (*Cormura, Peroptery x, Peronymus, Centronycteris,* and *Balantiopteryx*) under the name *Saccopteryx* and stated in a footnote that "As in many other cases, but to an exaggerated degree, I here unite a number of units almost universally called genera by modern mammalogists. They are however, manifestly and closely allied, cover less morphologic range than do many genera, and include so few species that generic separation has no practical value. This seems an obvious case, one of many, in which subgeneric rank has everything to be said for

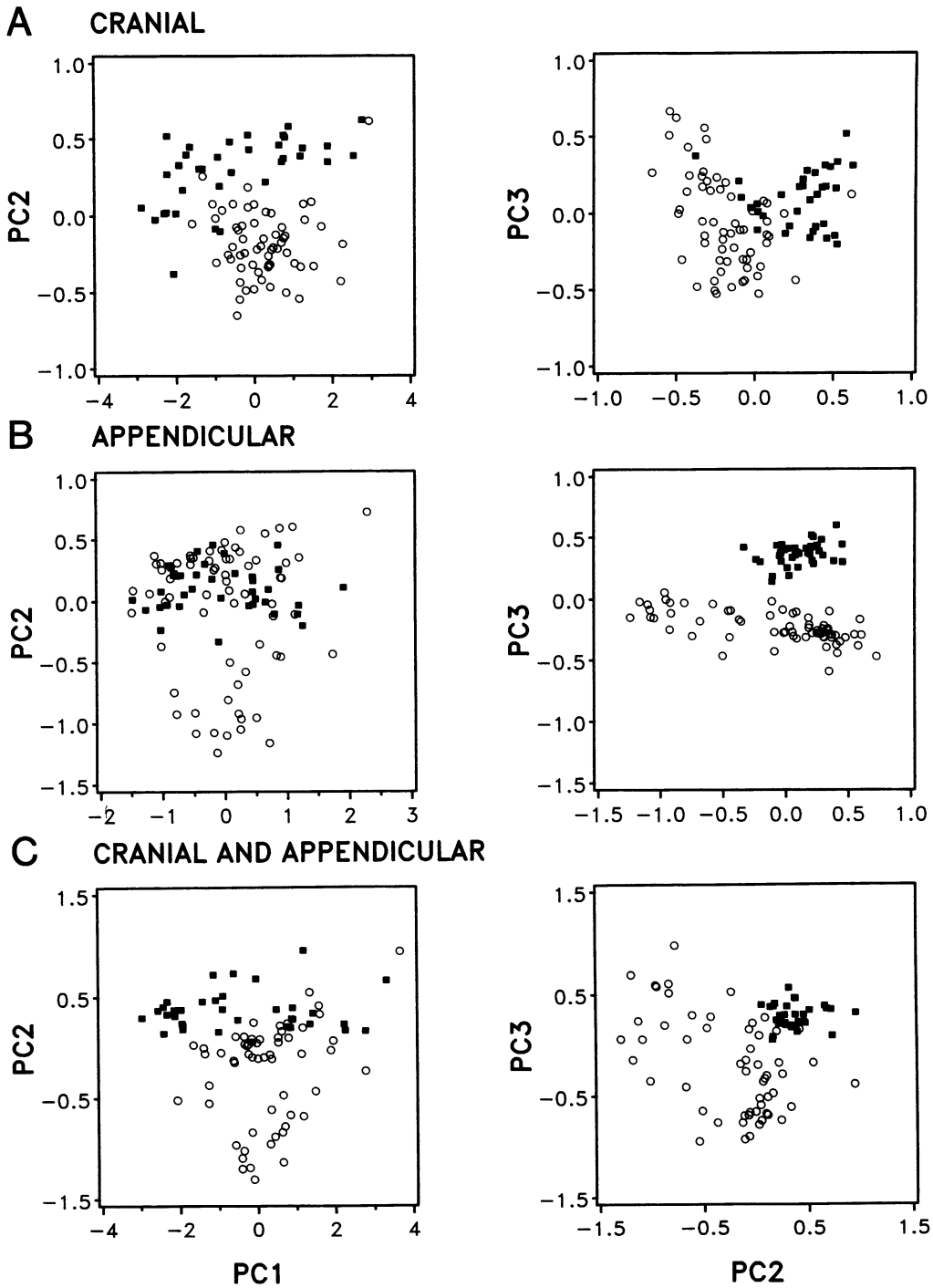

Fig. 3. Principal components analyses of the two-family data set, run on cranial measurements alone (**A**), appendicular measurements alone (**B**), and cranial and appendicular measurements together (**C**). Emballonurids are solid squares and molossids are open circles. Emballonurids are as variable as molossids in size (PC1, first column), but are much less variable in shape (PC2 and PC3).

it, both as better representing the real situation and as practically more convenient to everyone but the *Saccopteryx* specialist."

We investigated these qualitative claims of homogeneity by using the same 38 characters measured previously by Freeman (1981) for the family Molossidae and comparing entire families with one another. Both families are insectivorous, both occur worldwide, and for both we had over 75 percent of the total species in the family represented in our analysis. However, emballonurids are thought to be primitive and are placed in Koopman's infraorder Yinochiroptera, whereas the molossids are derived and are in the Yangochiroptera (Koopman, 1984a).

One way to compare size and shape diversity in two families is to compare the amount of variation that is and is not explained by the first principal component. In emballonurids, the total variation of characters is 3.51, of which 3.09 (88%) is explained by the first principal component. This leaves only 0.418 (12%) for the "shape" components. In molossids, the total variation is 1.95, with the first component explaining 1.182 (61%), and the remaining 0.769 (39%) on the "shape" axes. The conclusion that can be drawn is that the emballonurids are not as variable in shape as are the molossids, and this lack of variation can be seen in a variety of graphical representations.

We have run the two-family data set for variation in cranial measurements alone, appendicular measurements alone, and cranial and appendicular measurements together (fig. 3). The size component (PC1) in the cranial run shows that although there are more smaller-sized species of emballonurids than molossids, variation in size across the families is similar. Sizes among the two families from the appendicular measurement run show a similar degree of variation.

However, it is in the shape components, here represented by PC2 and PC3, that emballonurids show much less variation (fig. 3). Although molossids are more variable than emballonurids in shape in each of the three runs, the most dramatic difference in variation can be seen in the graph of the two shape components in the run with all 38 characters (fig. 3C; PC2 versus PC3). Based on these data, we conclude that emballonurids when compared to molossids morphometrically *are* a homogeneous group. This homogeneity may help explain why the emballonurids have been difficult to classify above the species level.

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Systematics of Emballonuroid Bats (Chiroptera: Emballonuridae and Rhinopomatidae), Based on Hyoid Morphology

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ABSTRACT

The hyoid musculature and hyoid apparatus of bats of the families Emballonuridae and Rhinopomatidae are described and compared with the hyoid morphology of selected specimens of bats of the families Nycteridae, Megadermatidae, and Rhinolophidae. The hyoid region of rhinopomatids is slightly modified, and the hyoid region of emballonurids is markedly modified from the primitive chiropteran hyoid morphology. In both families (and in nycterids and megadermatids), the omohyoid has shifted its origin medially from the scapula to the mid-clavicle. This permits the omohyoid to act as a primary tongue retractor, relieving the sternohyoid of this function. In rhinopomatids, the sternohyoid has been reduced to a weak, narrow muscle. In emballonurids, the sternohyoid has remained robust, but has developed a unique attachment to the posterior larynx. It appears to function in emballonurids as an extrinsic laryngeal muscle. A cladistic analysis of the hyoid data reveals two major clades within the Emballonuridae: the first contains *Taphozous* and *Saccolaimus* and the second contains *Emballonura, Mosia, Coleura,* and all New World genera. Within the latter clade, the genera *Emballonura, Mosia,* and *Coleura* compose a clade distinct from the New World genera. Within the New World clade there are two major lines: a line leading to *Rhynchonycteris* and *Diclidurus,* and a line leading to *Balantiopteryx, Saccopteryx, Cormura, Peropteryx,* and *Peronymus.* The phylogeny presented here agrees well with a recently published emballonurid phylogeny produced from karyotypic and electrophoretic/immunological data.

INTRODUCTION

Bats of the families Emballonuridae, Craseonycteridae, and Rhinopomatidae compose the superfamily Emballonuroidea, one of four superfamilies presently recognized within the suborder Microchiroptera (Weber, 1928; Koopman, 1984). Rhinopomatids and craseonycterids have a limited or nonexistent fossil record, but emballonurids are known from the late Eocene to early Oligocene of Europe in the form of the extant genus *Taphozous* and the extinct genus *Vespertiliavus.* Emballonurids are a taxonomically diverse and biogeographically widespread family. There are 15 genera containing about 50 species, compared with the smaller Rhinopomatidae (1 genus with 3 species) and Craseonycteridae (1 genus containing 1 species). The emballonurids are essentially pan-tropical in distribution (with the exception of Saharan Africa) and are noteworthy in having reached a number of the smaller island groups in the Indian Ocean and western Pacific.

Two previous studies—Barghoorn (1977) using cranial morphology and Robbins and Sarich (1988) using protein molecular data—have attempted to work out relationships between genera of emballonurid bats. Both studies agreed in concluding that the Old World genera *Taphozous* and *Saccolaimus* compose a clade that is a sister group of all

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the remaining emballonurid genera. Within the remaining genera, Barghoorn (1977) concluded that the genus *Emballonura* is on its own monogeneric line, and that the group containing the Old World *Coleura* and the New World genera is a sister group of *Emballonura*. Barghoorn recognized two clades within the *Coleura*–New World group, and suggested that *Coleura* is most closely related to the New World genera *Peropteryx, Peronymus,* and *Balantiopteryx*. This arrangement, while not impossible, is controversial because it places the African–Arabian–Seychelle Island genus *Coleura* within a group of highly derived New World genera, a group that excludes other highly derived New World emballonurids.

On the other hand, Robbins and Sarich (1988) concluded that a clade containing the Old World genera *Coleura* and *Emballonura* is a sister group of the clade containing all the New World emballonurid genera. This conclusion is more comforting from a biogeographic perspective because it places the Old World genera and New World genera in their expected groupings. Within the New World genera, Robbins and Sarich (1988) concluded that *Peropteryx* and *Peronymus* are related closely and that both genera are related to *Cormura*. The remaining five New World genera could not be grouped with confidence, and Robbins and Sarich's final cladogram contained an unresolved hexachotomy.

The two previous studies of emballonurid hyoid region anatomy (Sprague, 1943; Wassif and Madkour, 1968–69) gave no indication that the hyoid region was markedly modified in emballonurids. As the present study proceeded, it became apparent that the data obtained could be used to construct a cladogram for emballonurid bats, and possibly a cladogram for all emballonuroid genera. The purpose of this work is to describe the hyoid anatomy of representative specimens of all genera of emballonurid bats, except for the few genera (e.g., *Cyttarops*) for which fluid-preserved specimens are presently not available. Data are used to construct a cladogram, which is compared to the two previously published cladograms (Barghoorn, 1977; Robbins and Sarich, 1988). The genus *Rhinopoma* is also included, giving virtually complete coverage of the superfamily Emballonuroidea, except for the genus *Craseonycteris,* which remains unavailable despite ongoing efforts by the senior author to acquire permission to dissect at least one specimen. A few selected specimens of rhinolophid, megadermatid, and nycterid bats are described for purposes of outgroup comparison, though a more detailed study of these families, now in progress, will be published later.

Materials and Methods

Fluid-preserved museum specimens were dissected, and drawings were made of all dissections. From the initial pencil drawings, selected drawings were inked. The specimens came from the following institutions: AMNH, American Museum of Natural History, New York, NY; FMNH, Field Museum of Natural History, Chicago, IL; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. The following species and specimens were examined: **Family Emballonuridae:** *Balantiopteryx plicata:* AMNH 144598, 144600; *Coleura afra:* AMNH 188268, 188269, 237325; *Cormura brevirostris:* AMNH 123996 (skull extracted, some hyoid muscles absent), 143781, 244491; *Diclidurus albus:* FMNH 88235; *D. scutatus:* AMNH 95779 (skull extracted); *D.* sp.: FMNH 95364; *Emballonura alecto:* FMNH 80373, 80375; *E. beccarii:* AMNH 257111; *E. monticola:* AMNH 216794; *E. nigrescens:* AMNH 143879, 144057; *E. raffrayana:* AMNH 193598, 193599, 193604; *E. semicaudata:* AMNH 68833; *Peronymus leucopterus:* USNM 339559; *Peropteryx kappleri:* AMNH 239219, 239225; *P. macrotis:* AMNH 209230; *Rhynchonycteris naso:* AMNH 63661, 142896, 170622, 243707; *Saccolaimus peli:* AMNH 86904; *Saccopteryx bilineata:* AMNH 245303, 245305, 245307; *Taphozous melanopogon:* AMNH 237735, 237736; *T. nudiventris:* AMNH 208127; FMNH 111121. **Family Rhinopomatidae:** *Rhinopoma hardwickei:* AMNH 217292, 217296; *R. microphyllum:* AMNH 212070. **Family Rhinolophidae:** *Hipposideros armiger:* AMNH 112767; *H. diadema:* AMNH 206744; *Rhinolophus euryotis:* AMNH 158461. **Family Megadermatidae:** *Megaderma spasma:* AMNH 247252. **Family Nyc-**

teridae: *Nycteris thebiaca:* AMNH 245150, 245154.

Outgroup comparisons to determine character polarity within the Emballonuroidea were made not only with selected specimens of the families Rhinolophidae, Megadermatidae, and Nycteridae but also with New World phyllostomoid bats described previously by the senior author (Griffiths, 1978b; 1982).

ACKNOWLEDGMENTS

We thank Dr. Karl F. Koopman of the American Museum of Natural History for his helpful comments, critiques, advice, and encouragement during the course of this study. Karl has been a good friend and mentor to the senior author, and it is with pleasure that we dedicate this work to him. We thank Dr. Bruce Patterson of the Field Museum of Natural History and Dr. Charles Handley of the National Museum of Natural History for the loan of specimens unavailable at the American Museum. Dr. Lynn W. Robbins of Southwest Missouri State University and Dr. James M. Ryan of Hobart and William Smith Colleges reviewed the typescript of this paper and made suggestions that greatly improved it. Portions of this study were supported by two Faculty Development grants to TAG from Illinois Wesleyan University.

DESCRIPTION OF THE HYOID APPARATUS

In *Rhinopoma,* the basihyal element of the hyoid apparatus is in the form of a transverse cylindrical bar, with a large, rounded process projecting anteriorly (fig. 3). The thyrohyals are spatulate in shape, and appear to be strongly attached (though not fused) to the basihyal. In the anterior cornu, the ceratohyal (= hypohyal of Sprague [1943] and Wassif and Madkour [1968–69]) is a small element that articulates with the basihyal and epihyal by freely movable synchondral joints. The epihyal (= ceratohyal of Sprague [1943] and Wassif and Madkour [1968–69]) is much larger. It articulates by synchondrosal joint with a long, slender, curved stylohyal. The stylohyal extends laterally and posteriorly to the posterolateral rim of the auditory bulla. It terminates in a flattened paddle.

The hyoid apparatus of the emballonurids examined is similar, with the following exceptions. In all emballonurids except *Diclidurus,* the basihyal element is roughly diamond-shaped, with sharp points projecting anteriorly and posteriorly. In the New World genera *Balantiopteryx, Saccopteryx, Cormura, Peropteryx,* and *Peronymus,* the diamond shape is present, but the anterior point of the diamond is blunted and the posterior point is elongated (figs. 11, 13, 15). In *Diclidurus,* the basihyal morphology is unique. The anterior surface is curved, and there are two small processes projecting posteriorly, one to each side of the midline (fig. 9). In all emballonurids, the ceratohyal is smaller than the epihyal. Generally the ceratohyal is about one-half the size of the epihyal, though this varies somewhat within genera. The stylohyal terminates in an expanded paddle on the posterolateral edge of the auditory bulla.

In megadermatids, the hyoid apparatus is similar, with the following exceptions. The basihyal is shaped like a bar, with a prominent ventral process projecting from its ventral midpoint. The thyrohyals are fused to the basihyal, and the epi- and ceratohyals are large, well-developed elements. In nycterids, the basihyal is also bar-shaped, but it is much less robust. The other elements are similar to those of megadermatids, but much less robust. In rhinolophids, there is some variation. In *Hipposideros armiger,* the basihyal is roughly butterfly-shaped, with large thyrohyals that are strongly fused to the basihyal. The other elements of the anterior cornu are similar to those described above, except that the stylohyal has a large, distal "foot" expansion lying on the ventral surface of the auditory bulla. In *Triaenops* and *Rhinonycteris,* the hyoid apparatus is very different. The basihyal is more rectangular, with a large depression in the ventral surface. The thyrohyals are fused, but they are long and thin. The ceratohyal is very reduced, and the epihyal and stylohyal elements are very thin. The distal "foot" of the stylohyal is fused to the ventral surface of the auditory bulla.

Though the structure of the larynx is not specifically a part of this study, certain details of laryngeal morphology are important and need be mentioned here. All larynges studied have a complex cricothyroid muscle and a

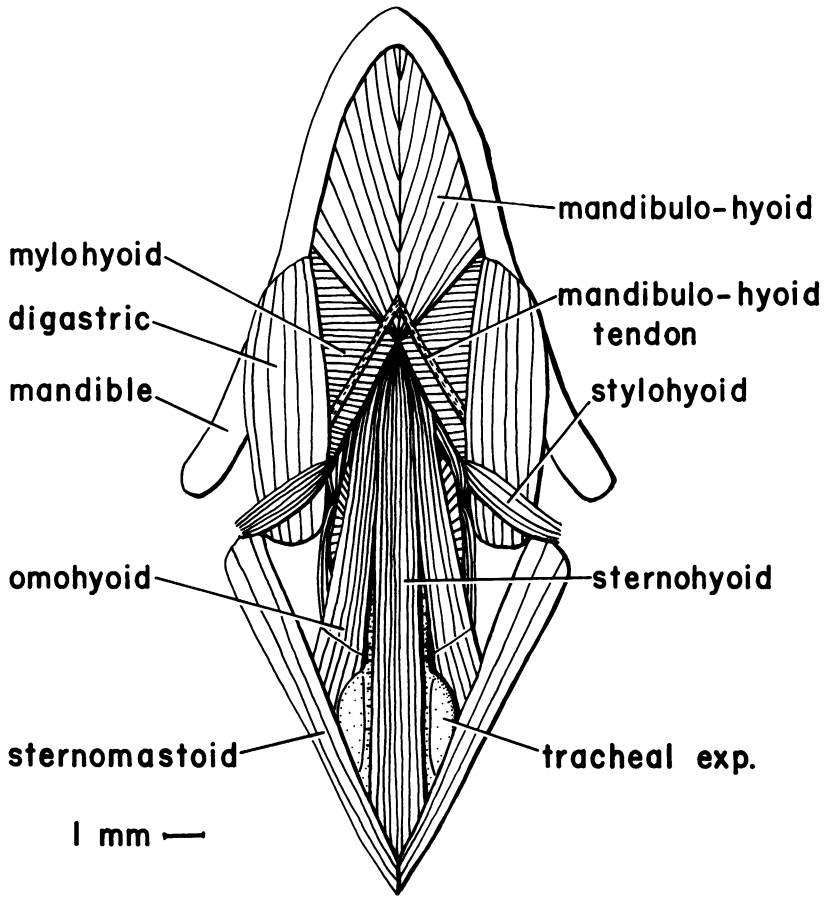

Fig. 1. Ventral view of the undissected hyoid region of *Rhinopoma hardwickei.*

prominent cricoid cartilage visible on the ventral surface. The larynx of *Rhynchonycteris* is unusual in that the posterior cricothyroid fibers cover the posterior cricoid cartilage (fig. 6). In a number of genera, there is a postlaryngeal chamber formed by expansion of tracheal rings. In *Rhinopoma,* the expansion is in rings 6–16. In *Emballonura* and *Coleura,* the expansion is in tracheal rings 2–10 (approximately). Finally, in *Peropteryx* and *Peronymus* there is a tracheal expansion that involves primarily ring number 1, though rings 2–5 also open into the lumen of the expansion.

DESCRIPTION OF THE MUSCLES

For each muscle described below, the generalized emballonurid condition is described first under "Origin" and "Insertion." If there is no generalized condition, the most plesiomorphic condition is described. Following this, variation from the generalized condition (including the sometimes peculiar morphology of *Rhinopoma*) is described under "Other Emballonuroids." Finally, under "Other Yinochiroptera," specimens are described from the families Rhinolophidae, Nycteridae, and Megadermatidae.

Branchiomeric Musculature

Mylohyoid Group

Muscles of this group are innervated by the mylohyoid nerve, a branch of N. mandibularis, which is in turn a branch of N. trigeminus (V).

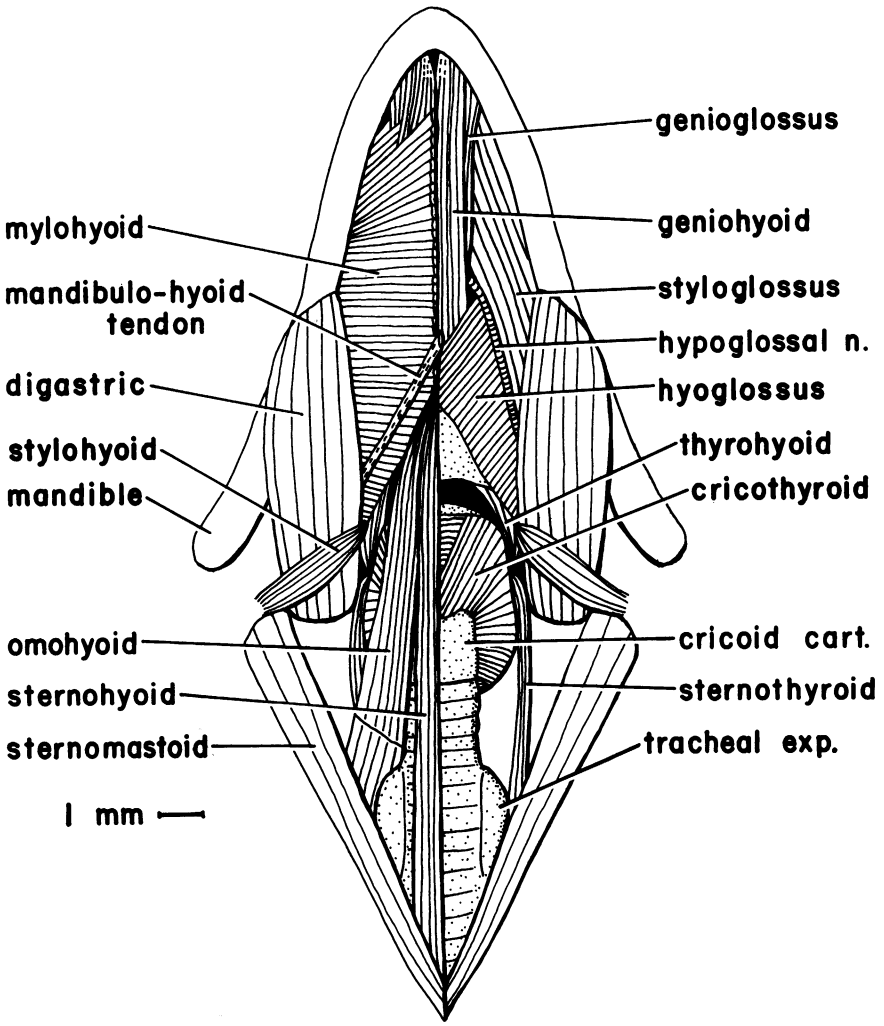

Fig. 2. Ventral view of the hyoid region of *Rhinopoma hardwickei.* Deeper structures are shown on the right (the specimen's left) side. The manidibulo-hyoid has been removed on both sides.

M. mylohyoideus
Figures 1, 2, 4, 6, 8, 10, 12, 14

ORIGIN: From the medial surface of the mandible for much of the length of the mandibular body.

INSERTION: Into its antimere along the ventral midline raphe and, posteriorly, onto the ventral tip of the basihyal and the ventral surface of the thyrohyal.

OTHER EMBALLONUROIDS: This muscle is the same in all emballonuroids dissected, with the following minor exceptions. In *Rhinopoma,* the mylohyoid does not extend as far anteriorly, with the result that the deeper muscles are visible (see fig. 2). In the single specimen of *Rhynchonycteris* dissected and in all *Diclidurus* (figs. 6, 8), the senior author was unable to find any mylohyoid fibers inserting on the thyrohyal; the posteriormost fibers inserted exclusively on the basihyal. Also in *Diclidurus,* the anteriormost fibers of the mylohyoid were exceptionally thick.

OTHER YINOCHIROPTERA: In all rhinolophids and megadermatids, the mylohyoid differs in two respects. In both families, it inserts on the basihyal alone (not on the thyrohyal element) and the mylohyoid does not continue very far anteriorly after passing deep to the mandibulo-hyoid (see below). In *Nycteris,*

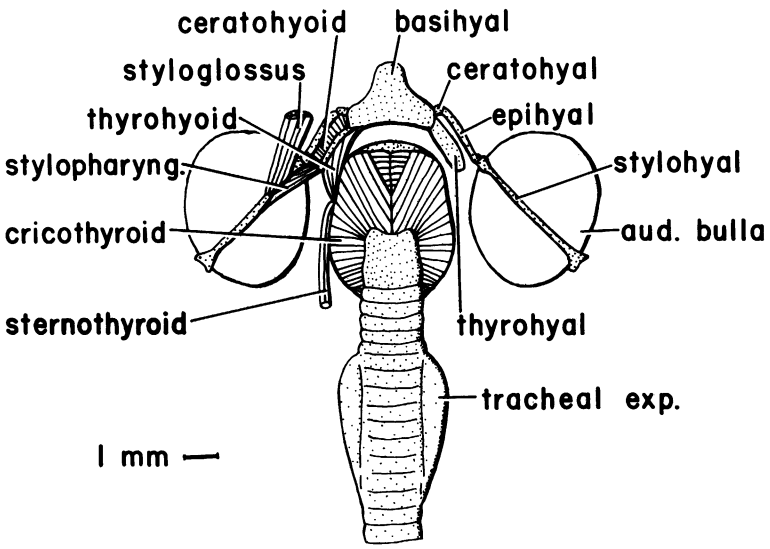

Fig. 3. Ventral view of the deep hyoid muscles, the hyoid apparatus, and the larynx of *Rhinopoma hardwickei.*

the muscle is similar to the emballonuroid mylohyoid, with one difference. As in the other rhinolophoid families, it inserts on the basihyal but not on the thyrohyal to any great degree. There is no mandibulo-hyoid in nycterids, and the mylohyoid continues anteriorly to the mandibular symphysis.

COMMENTS: The mylohyoid does not insert on the thyrohyal in the three rhinolophoid families examined, or in other families of Microchiroptera outside the Yinochiroptera (Sprague, 1943; Griffiths, 1982). Thus, it is possible that insertion on the thyrohyal is the derived (apomorphic) condition for emballonuroid bats. If this is the case, insertion on the thyrohyal would be a synapomorphy of rhinopomatid and emballonurid bats. We have chosen not to incorporate this character in our cladogram (fig. 16) because we believe that it is equally likely that insertion on the thyrohyal is a symplesiomorphy shared by *Rhinopoma* and most of the emballonurid genera. However, there is no question that within the family Emballonuridae, the loss of the mylohyoid insertion on the thyrohyal in *Rhynchonycteris* and *Diclidurus* is the derived condition relative to the rest of the family, and we have incorporated this as character state 12 in figure 16.

In all emballonurids (including *Taphozous*), the mylohyoid is thickest anteriorly and posteriorly and thinnest between these two extremes. However, it is never apoeneurotic or broken into distinct anterior and posterior parts, as was found in some phyllostomid bat genera (Griffiths, 1982).

M. mylohyoideus profundus

This muscle is absent in all bats dissected. The term "mylohyoideus profundus" was coined by Griffiths (1978a) to describe a deep, posterior piece of the mylohyoid that seemed to have become a separate muscle in phyllostomid bats. This deep mylohyoid apparently had remained attached to the basihyal as the remainder of the mylohyoid was displaced superficially by the development of a "free-floating" sterno-glossus complex. In *Cormura,* a few fibers of the mylohyoid pass dorsal to the insertion of the sternohyoid and omohyoid to insert on the basihyal. However, the fibers are continuous with the remainder of the mylohyoid, and in no way do they constitute a separate muscle.

Griffiths (1982) mistakenly used the term "mandibulo-hyoideus" to describe the mylohyoideus profundus, believing that Sprague (1943) had previously described the deep mylohyoid under that term. All written de-

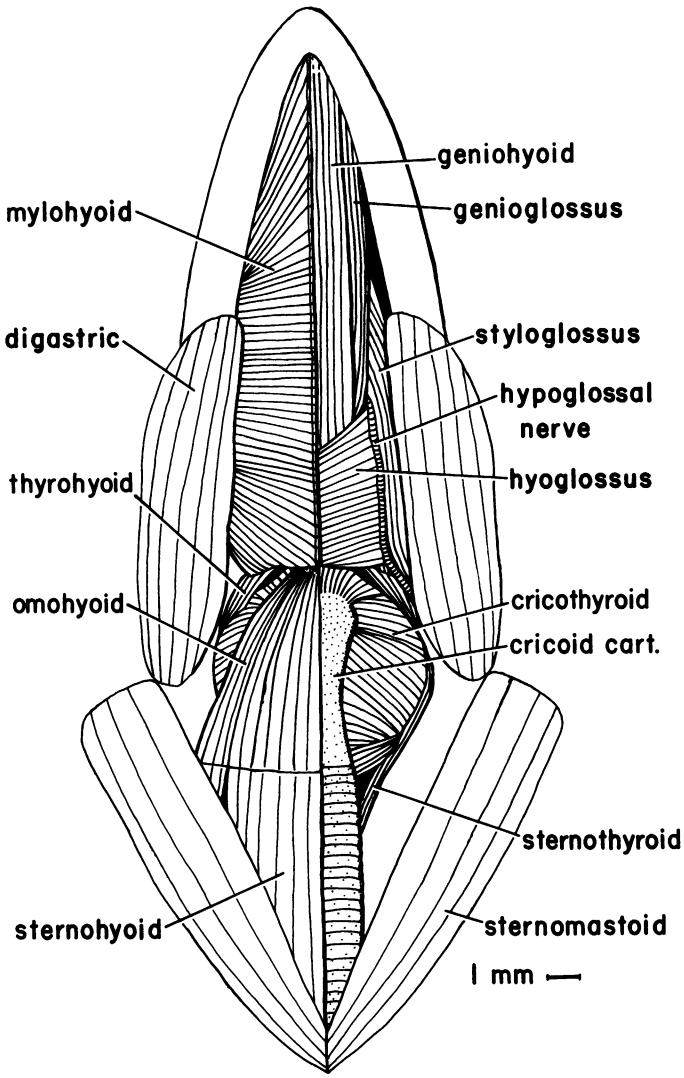

Fig. 4. Ventral view of the hyoid region of *Taphozous nudiventris*. Deeper structures are shown on the right of the illustration.

scriptions and figures in Griffiths (1982) are accurate, but wherever the term "mandibulo-hyoideus" is used in that paper, "mylohyoideus profundus" should be substituted.

M. mandibulo-hyoideus
Figure 1

This muscle is present in rhinopomatids, megadermatids, and rhinolophids, but is completely absent in all other families examined. In each case, the origin is from the medial surface of the anterior mandibular body. In rhinopomatids, the muscle passes posteriorly, narrowing as it does so, to insert on the basihyal bone. However, it is also strongly attached on each side to a tendon that passes posteriorly and laterally across the opposite side, finally running deep to the digastric (figs. 1, 2). On the deep surface of the digastric, the tendon strongly attaches to the dorsal part of the raphe between the anterior and posterior bellies of the digastric. The muscle lies superficial to the anterior part of the mylohyoid, covering it.

In megadermatids and rhinolophids, no

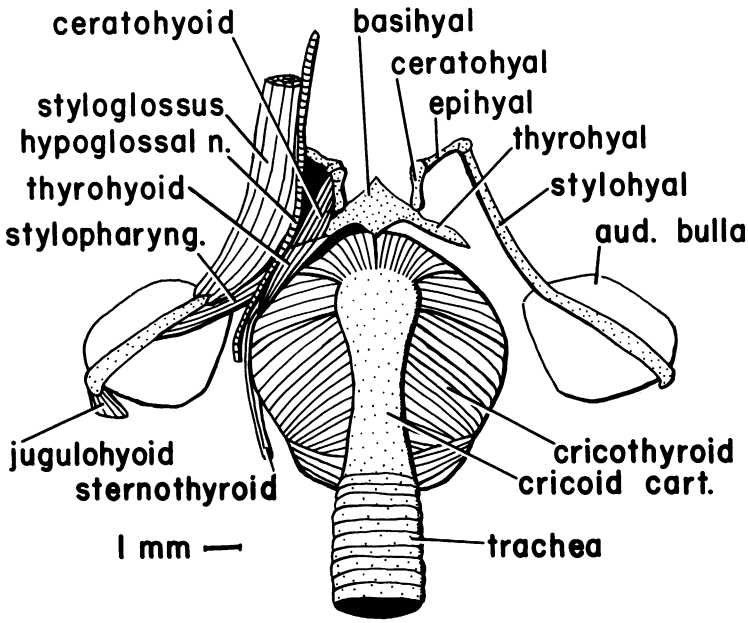

Fig. 5. Ventral view of the deep hyoid structures and the larynx of *Taphozous nudiventris*.

such tendon exists. The muscle inserts into the connective tissue midline raphe of the mylohyoid/geniohyoid. Connective tissue of the raphe is arranged in such a fashion that the mandibulo-hyoid could indirectly pull the basihyal anteriorly.

COMMENTS: Sprague (1943) suggested that the mandibulo-hyoid was a superficial fasciculus of the mylohyoid, and discussed its occurrence in other mammals. Presence of the muscle in rhinopomatids, megadermatids, and rhinolophids is probably the plesiomorphic state (Sprague, 1943), but its loss in emballonurids and nycterids cannot be considered necessarily a synapomorphy, as the mandibulo-hyoid is absent in many mammal groups that must have lost the muscle independently.

Because a mandibulo-hyoid is not present in any emballonurid genus described, it would be of interest to ascertain if *Craseonycteris* does or does not have the muscle. The presence or absence of the muscle in *Craseonycteris* would likely reveal much about the relationships of the three families of bats in the superfamily Emballonuroidea. There is a large branch of the mylohyoid nerve that apparently has developed to supply this muscle.

As we indicated above, Griffiths' (1982) use of "mandibulo-hyoid" was in error.

HYOID CONSTRICTOR GROUP

Muscles of this group are innervated by branches of N. facialis (VII).

M. stylohyoideus

Figures 1, 2, 6, 8, 10, 12, 14

ORIGIN: By short tendon from the posterior edge of the expanded lateral tip of the stylohyal elements.

INSERTION: The muscle passes around the ventral surface of the digastric to insert on the lateral tip of the thyrohyal.

OTHER EMBALLONUROIDS: The muscle is completely absent in *Taphozous* and *Saccolaimus*. The muscle is present in all other emballonuroids examined, including *Rhinopoma*. In all specimens of *Peropteryx* and *Peronymous* dissected, the insertion is shifted medially. Rather than inserting on the tip of the thyrohyal, the muscle inserts by tendon onto the lateral basihyal, just medial to the basihyal/thyrohyal articulation.

OTHER YINOCHIROPTERA: The muscle is the same in megadermatids and nycterids. We

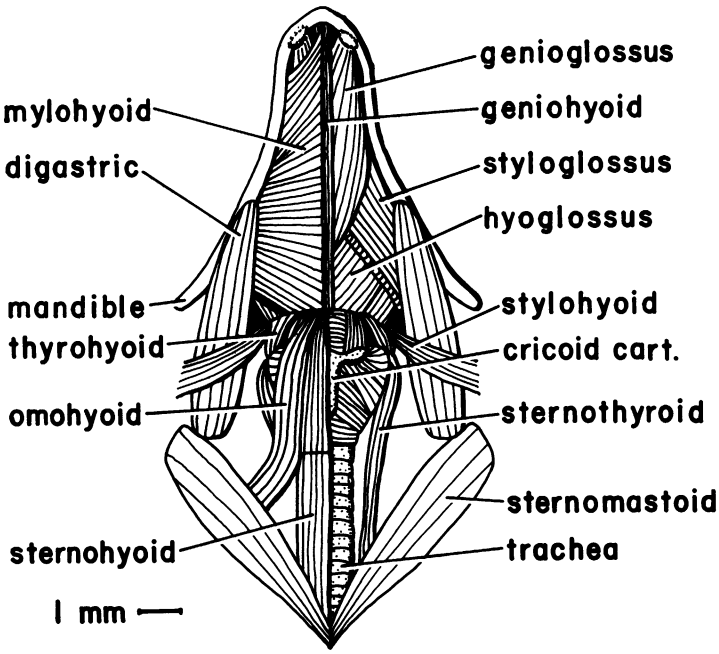

Fig. 6. Ventral view of the hyoid region of *Rhynchonycteris naso.* Deeper structures are shown on the right of the illustration.

do not agree with Sprague (1943), who reported this muscle absent in megadermatids. The stylohyoid appears to be absent in rhinolophids, though there is a peculiar small muscle that runs from the medial surface of the expanded lateral "foot" of the stylohyal to the lateral tip of the thyrohyal, just as the stylohyoid is supposed to do. This cannot be a true stylohyoid, however, because it does not curve medially around the ventral digastric; rather, it runs directly in a short, straight run from its origin to its insertion. There is no way for this muscle to be derived from a proper stylohyoid, as it would have to pass through the digastric to arrive in its present position. We presume that this new muscle is a piece of an adjacent muscle (probably the stylopharyngeus) that attached to the lateral thyrohyal and then detached from the parent muscle.

COMMENTS: The unusual insertion of the muscle in *Peropteryx* and *Peronymus* and the complete absence of the muscle in all specimens of *Taphozous* and *Saccolaimus* are clearly synapomorphic character states that support a close phylogenetic relationship between the former two genera, and between the latter two genera.

M. jugulohyoideus
Figure 5

ORIGIN: From the paroccipital shelf just posterior to the auditory bulla.

INSERTION: Onto the expanded lateral tip of the stylohyal.

OTHER EMBALLONUROIDS: This muscle is present, but very reduced, in *Rhinopoma.* It is present in *Taphozous, Saccolaimus, Emballonura, Coleura,* and *Mosia.* It is absent in all other emballonurid genera (replaced by connective tissues) or at best reduced to a few faint muscle fibers embedded in connective tissue (e.g., in some specimens of *Rhynchonycteris*).

OTHER YINOCHIROPTERA: In rhinolophid and megadermatid bats, the muscle is robust and similar to the description given above. In nycterids, the origin and insertion are the same, but the muscle is proportionately smaller.

COMMENTS: We conclude that the reduc-

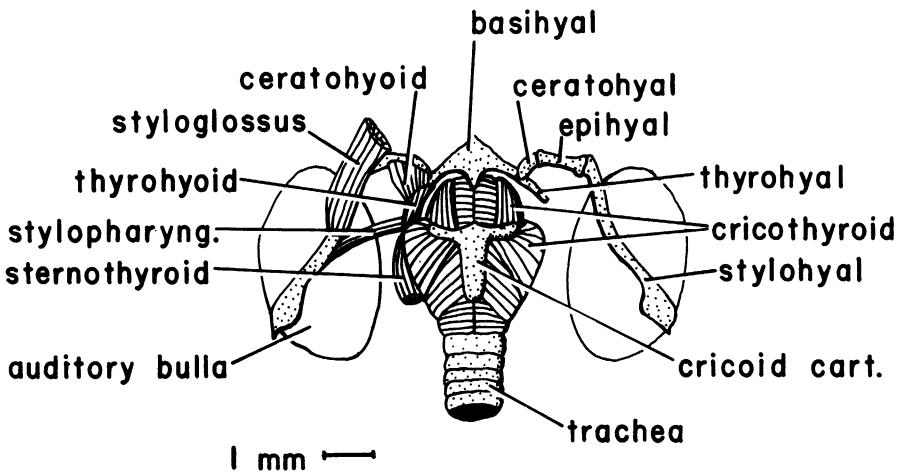

Fig. 7. Ventral view of the deep hyoid structures and the larynx of *Rhynchonycteris naso.*

tion in size (character state 4 in fig. 16) and the complete absence of the muscle (character state 7) in a number of emballonurid genera is a synapomorphy uniting those genera.

M. sphincter colli profundus

This muscle is completely absent in all emballonuroids (rhinopomatids and emballonurids).

OTHER YINOCHIROPTERA: The muscle is absent in nycterids. It is present in *Megaderma,* where it originates from the raphe bisecting the sternohyoid (not from the basihyal raphe). It is extremely robust, fanning out anteriorly and laterally from its origin to insert on the deep surface of the skin just ventral to the ear. The muscle is absent in all species of rhinolophids examined, except that in *Hipposideros armiger* there were faint traces of a vestigial sphincter colli originating from the basihyal raphe. The muscle was extremely difficult to see, being confined to a few fibers embedded in the heavy fascia of the neck. It proved impossible to trace the path of these vestigial fibers.

GLOSSOPHARYNGEAL GROUP

Muscles of this group are innervated by branches of N. glossopharyngeus (IX).

M. stylopharyngeus
Figures 3, 5, 7, 9, 11, 13, 15

ORIGIN: From the medial surface of the stylohyal element, slightly lateral and posterior to the origin of the styloglossus muscle.

INSERTION: Into the lateral wall of the pharynx, passing into the pharynx wall just anterior to the course of the thyropharyngeus.

OTHER EMBALLONUROIDS: This muscle is the same in all emballonuroid genera, including *Rhinopoma.*

OTHER YINOCHIROPTERA: The muscle is the same in all bats examined.

M. ceratohyoideus
Figures 3, 5, 7, 9, 11, 13, 15

ORIGIN: From the anterior surface of the thyrohyal element.

INSERTION: Onto the posterior surface of the ceratohyal and the posterior surface of the epihyal.

OTHER EMBALLONUROIDS: The insertion of this muscle is quite variable. In *Rhinopoma,* it is the same as described above. In *Taphozous nudiventris,* the insertion is onto the posterior surface of the ceratohyal, but not onto the epihyal to any great extent. In *Balantiopteryx,* the insertion is onto the posterior surfaces of the entire ceratohyal and the medial one-third of the epihyal. In *Cormura, Diclidurus, Peropteryx, Peronymus, Rhynchonycteris, Saccolaimus, Saccopteryx,* and *Taphozous melanopogon,* the insertion is nearly the same, but extends a bit further laterally,

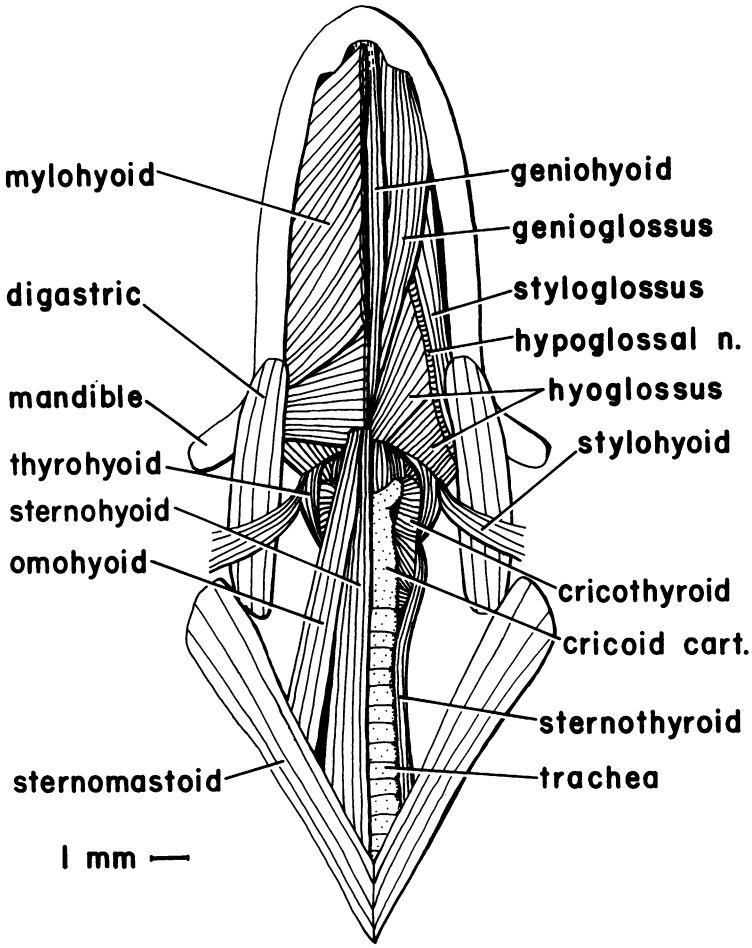

Fig. 8. Ventral view of the hyoid region of *Diclidurus* sp. (FMNH 95364). Deeper structures are shown on the right of the illustration.

the muscle inserting on the medial one-half of the epihyal. In *Coleura, Emballonura,* and *Mosia,* the insertion is onto the posterior surfaces of the entire ceratohyal, entire epihyal, and the medial tip of the stylohyal.

OTHER YINOCHIROPTERA: In megadermatids, the origin is the same but the insertion is onto the ceratohyal and the medial tip of the epihyal. In nycterids, the origin is the same, but the insertion is onto the posterior surface of the elongated ceratohyal (not onto other anterior cornu elements at all). In rhinolophids, the muscle is variable within the family. In *Hipposideros* and *Rhinolophus,* the muscle originates from the lateral tip of the thyrohyal and inserts on the lateral half of the epihyal and the medial quarter of the stylohyal. In *Rhinonycteris* and *Triaenops,* the muscle is completely absent.

COMMENTS: As the senior author has stated previously (Griffiths, 1982; Griffiths et al., 1991), it is very difficult to know how much significance to assign to the variation observed in this muscle. There are two problems. First, it is very difficult to determine with certainty what the plesiomorphic condition is in this muscle. Sprague (1943) also suggested that the primitive condition for the Chiroptera was as we have stated above, but there is so much variation within the Chiroptera (Sprague, 1943; Griffiths, 1982, 1983) that it is impossible to use outgroups to determine with certainty the answer to this important question. Second, it would seem as

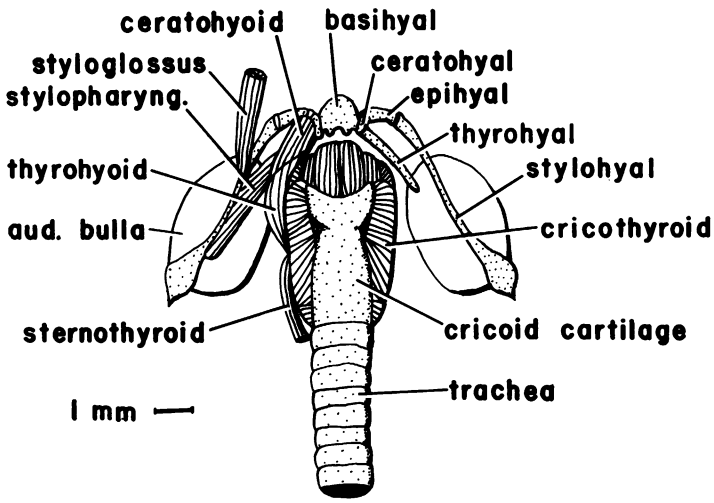

Fig. 9. Ventral view of the deep hyoid structures and the larynx of *Diclidurus* sp.

though the insertion of this muscle could vary quite easily. The anterior cornu of the hyoid apparatus is a continuous, flexible structure. A muscle that inserts on the ceratohyal element could extend its insertion to the epihyal merely by crossing the synchondral joint between the two elements. A minor change in muscle size would seem to accomplish this easily. Alternatively, a change in the relative size of the cornu elements might accomplish the same thing if the muscle remained constant in size.

Though the issue is far from settled, it appears that there is one synapomorphic character state that can be trusted: the extended insertion found in *Emballonura, Coleura,* and *Mosia.* This extended insertion is not found in any of the other bats in this study (including *Rhinopoma* of the Rhinopomatidae), nor is it found in other families of bats considered to be closely related. Specifically, in *Nycteris* and *Megaderma,* the ceratohyoid attaches to the ceratohyal (= "hypohyal" of Sprague) alone (Sprague, 1943). In *Rhinolophus* and *Hipposideros,* the ceratohyoid attaches to the epihyal (Sprague's "ceratohyal") and to the medial tip of the stylohyal (Sprague, 1943), but not at all to the medialmost element. Thus, the extended insertion appears to be a valid synapomorphic character state shared by the genera *Emballonura, Coleura,* and *Mosia.*

Interestingly, there seems to be some variation within the genus *Taphozous.* With further study, this variation might prove useful in working out relationships within this morphologically diverse genus.

Pharyngeal Constrictor Group

Muscles of this group are innervated by branches of N. vagus (X).

M. hyopharyngeus

Origin: From the fascia in the vicinity of the pterygoid processes.

Insertion: Into the dorsal midline of the pharynx, deep to and anterior to the fibers of the thyropharyngeus.

Other Emballonuroids and Yinochiroptera: This muscle is the same in all bats examined.

M. thyropharyngeus

Origin: In *Taphozous,* from the dorsal surface of the tip of the thyrohyal bone.

Insertion: Into the dorsal midline of the pharynx.

Other Emballonuroids and Yinochiroptera: This muscle is the same in all bats examined.

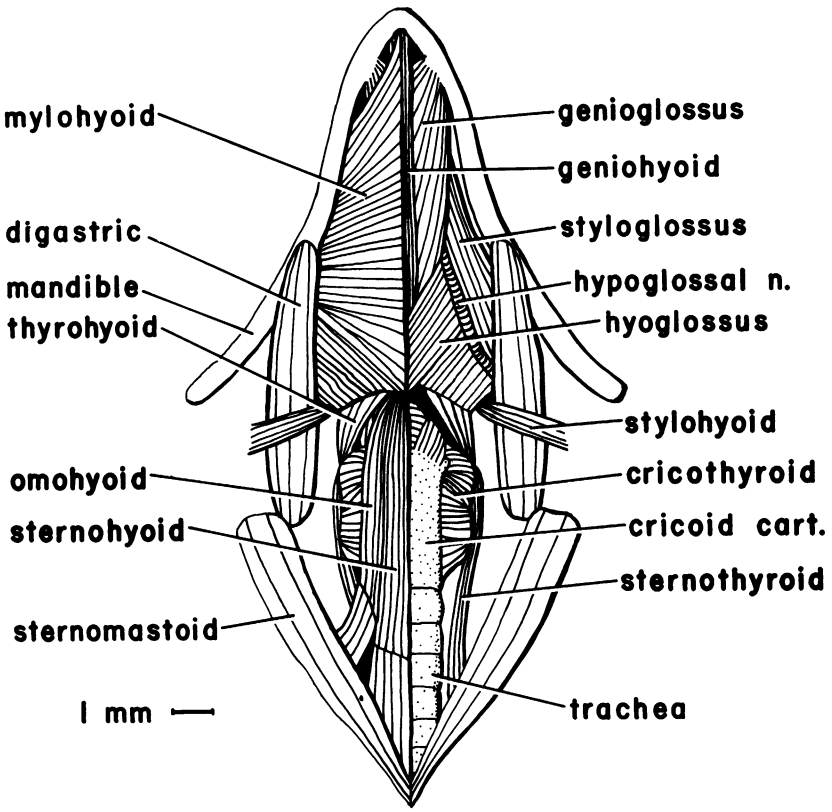

Fig. 10. Ventral view of the hyoid region of *Balantiopteryx plicata.* Deeper structures are shown on the right of the illustration.

M. cricopharyngeus

ORIGIN: From the lateral surface of the cricoid cartilage and from the dorsal surface of the posterior thyroid process.

INSERTION: Into the dorsal midline of the pharynx.

OTHER EMBALLONUROIDS AND YINOCHIROPTERA: This muscle is the same in all bats examined.

MYOTOMIC MUSCULATURE

LINGUAL GROUP

Muscles of this group are innervated by the N. hypoglossus (XII).

M. genioglossus

Figures 2, 4, 6, 8, 10, 12, 14

ORIGIN: From the posterior surface of the anterior mandible, just dorsal and slightly lateral to the origin of the geniohyoid.

INSERTION: Into the ventral surface of approximately the posterior one-half of the tongue; the most posterior fibers turn laterally and pass deep to the hyoglossus.

OTHER EMBALLONUROIDS: This muscle is the same in all emballonuroids examined. It is particularly robust in all emballonurids.

OTHER YINOCHIROPTERA: In nycterids and rhinolophids, the muscle is the same as described above. In megadermatids, the muscle is similar except that there is no sign of the posteriormost fibers turning laterally to pass under the hyoglossus.

COMMENTS: This muscle is very well developed in all emballonurid genera dissected. Because it is robust, and because the geniohyoid is reduced, the genioglossus protrudes laterally in such a fashion that most of it is visible lateral to the geniohyoid without further dissection. The muscle is so strong that, in most genera, a prominent mandibular "knob" has developed at its point of origin

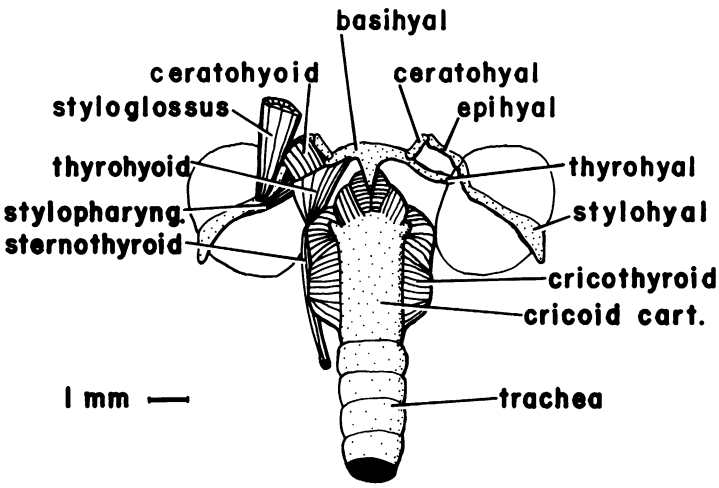

Fig. 11. Ventral view of the deep hyoid structures and the larynx of *Balantiopteryx plicata.*

(figs. 6, 8, 10, 14), apparently in response to the strong pull of the genioglossus.

M. hyoglossus
Figures 2, 4, 6, 8, 10, 12, 14

ORIGIN: From the ventrolateral part of the basihyal bone and from the ventral surface of the thyrohyal bone.

INSERTION: Into the posterolateral corner of the tongue, deep to the hypoglossal nerve and the styloglossus muscle.

OTHER EMBALLONUROIDS: Although the hyoglossus muscle itself does not change its attachment to the hyoid apparatus, a change in the relative size and shape of different parts of the hyoid apparatus causes this muscle to become modified within the family Emballonuridae. In *Rhinopoma, Taphozous, Saccolaimus, Coleura, Emballonura,* and *Mosia,* the muscle consists of a single, unbroken sheet that originates from both the basihyal and the thyrohyal elements. In all the New World emballonurid genera, the basihyal is elongated posteriorly, and the part of the hyoglossus that originates from the basihyal has expanded posteriorly along the elongation. This has resulted in a two-part hyoglossus: two distinct bellies that have a clear physical separation. In *Saccopteryx* and *Cormura,* the separation is especially evident (fig. 12).

OTHER YINOCHIROPTERA: In all nycterids and rhinolophids, the origin of this muscle is exclusively from the lateral surface of the basihyal; there is no attachment to the thyrohyals and no evidence of any lateral part of the hyoglossus. In megadermatids, the muscle initially appears to be similar, but upon dissection it turns out that something surprising has occurred in the evolution of this muscle. The muscle has an indirect, tendinous attachment to the basihyal, but its real origin is from the sternohyoid. The sternohyoid, geniohyoid, and hyoglossus muscles have "lifted off" the basihyal, retaining only a common tendinous attachment. This condition parallels closely the condition found in New World leaf-nosed bats (Griffiths, 1978a, 1982).

COMMENTS: Quite clearly, the elongation of the basihyal (with the accompanying division of the hyoglossus) is a synapomorphy shared by all New World emballonurid genera. We have incorporated this as character state 8 in figure 16. The genera *Saccopteryx* and *Cormura* share a further derivation of the condition (8+ in fig. 16). It is probable that the lack of a lateral hyoglossus in the three rhinolophoid families is a synapomorphy.

M. styloglossus
Figures 2–15

ORIGIN: From the ventral surface of the stylohyal element at about the point where it bends ventrally (about the midpoint).

INSERTION: Into the lateral surface of the tongue.

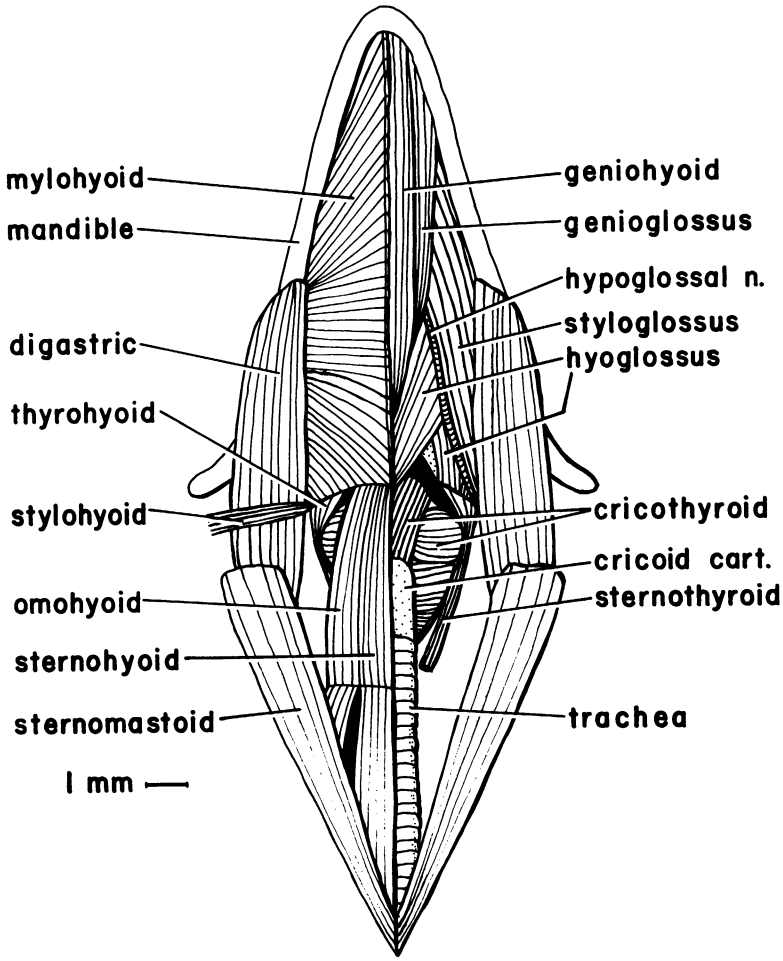

Fig. 12. Ventral view of the hyoid region of *Saccopteryx bilineata.* Deeper structures are shown on the right of the illustration.

OTHER EMBALLONUROIDS: This muscle is the same in all genera examined.

OTHER YINOCHIROPTERA: This muscle is the same in megadermatids, except that it enters the tongue quite far posteriorly. In nycterids, the muscle is the same as in emballonuroids. In rhinolophoids, there is some variation in the origin, but otherwise the muscle is similar to the emballonuroid condition. In *Rhinolophus* and *Hipposideros,* the origin is from the approximate midpoint of the stylohyal. In *Triaenops* and *Rhinonycteris,* the origin is more distally located, coming from the expanded "foot" of the stylohyal.

COMMENTS: Although this observation is of no value in working out phylogenetic relationships within the emballonuroids, it is worth noting that the styloglossus of emballonuroids takes origin from the stylohyal element at a very different point than in phyllostomids (Griffiths, 1982). In phyllostomids, the muscle originates from the expanded lateral tip of the stylohyal. In all emballonuroids examined, the origin is much more medially situated. This observation might prove useful in future studies of interfamilial relationships.

MEDIAL VENTRAL CERVICAL GROUP

The muscles of this group are innervated by a complex of nerves originating in the an-

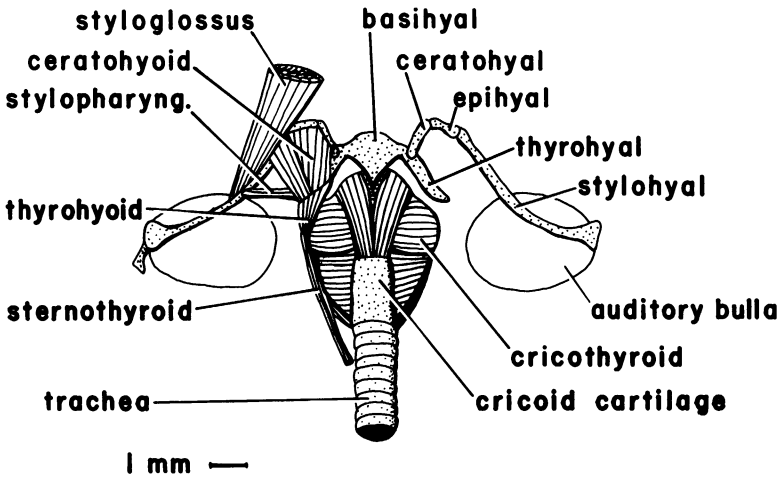

Fig. 13. Ventral view of the deep hyoid structures and the larynx of *Saccopteryx bilineata.*

terior cervical region, except for the geniohyoid, which appears to be innervated primarily by N. hypoglossus (XII).

M. geniohyoideus
Figures 2, 4, 6, 8, 10, 12, 14

ORIGIN: By tendon from the posterior surface of the mandible, just lateral to the mandibular symphysis.

INSERTION: Onto the anterior surface and ventral tip of the basihyal bone.

OTHER EMBALLONUROIDS: In *Rhinopoma,* the origin and insertion are the same, but the lateral fibers of the geniohyoid arise directly from the bone (not by tendon), while the medial fibers originate by tendon. The muscle is robust in *Rhinopoma,* and not fused to its antimere. The geniohyoid has the same origin and insertion in all emballonurid genera examined. However, the relative size of the geniohyoid varies within the family Emballonuridae. In *Taphozous* and *Saccolaimus,* the geniohyoid is a robust muscle that is loosely bound by connective tissue (not fused) to its antimere. In all other genera, the geniohyoid is reduced and is fused to its fellow geniohyoid for its entire length, except at the tendinous origin.

OTHER YINOCHIROPTERA: In nycterids, the muscle is similar to the general emballonurid condition described above. In rhinolophids, the muscle is similar to the emballonurid condition in all respects, except that in *Triaenops* and *Rhinonycteris* the origin is not by tendon, but rather by fleshy fibers. In megadermatids, the muscle has lost its direct attachment to the basihyal, becoming "free-floating" as described under hyoglossus above. The origin is entirely fleshy (nontendinous), and the muscle is fused with its antimere for its entire length.

COMMENTS: The reduced geniohyoid in *Emballonura, Coleura, Mosia,* and the New World genera appears to be a synapomorphy (table 1, character state 3). From a functional point of view in these bats, it would seem that it is not too important to provide anterior pull on the basihyal (thus the reduced geniohyoid), but very important to be able to protrude the tongue (accounting for the massive genioglossus with the reinforced point of origin).

M. sternohyoideus
Figures 1, 2, 4, 6, 8, 10, 12, 14

ORIGIN: By two slips, the medial from the anterior surface of the manubrium of the sternum, and the lateral from the proximal head of the clavicle (closely associated with the origin of the sternothyroid).

INSERTION: Onto the posterior edge of the basihyal bone. However, in *Taphozous* and *Saccolaimus,* the sternohyoid is loosely attached to the region of the first tracheal ring/cricoid cartilage by connective tissue fibers. In all other emballonurid genera, the second-

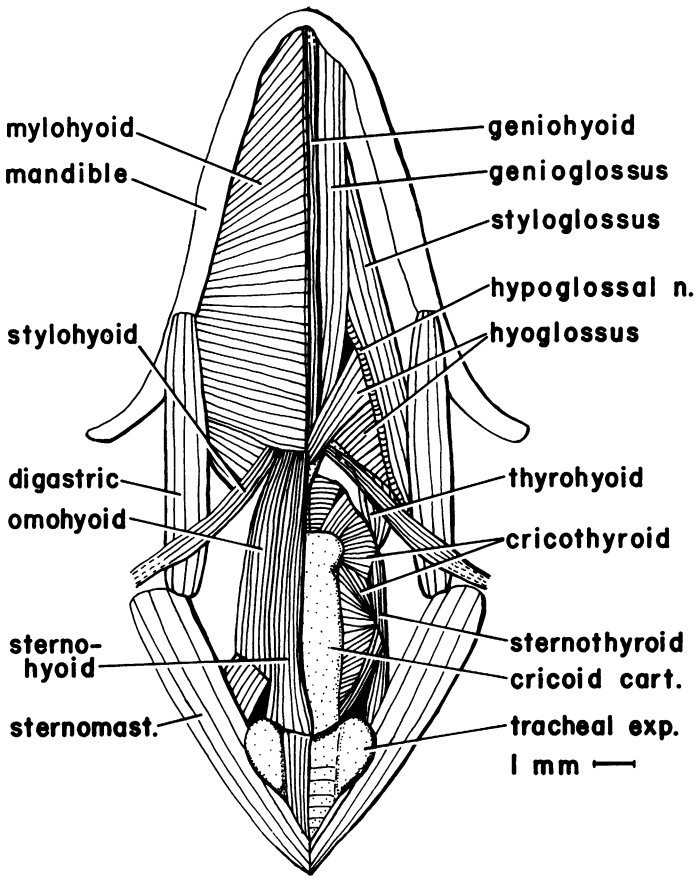

Fig. 14. Ventral view of the hyoid region of *Peropteryx kappleri.* Deeper structures are shown on the right of the illustration.

ary attachment to the tracheal ring/cricoid is much stronger, creating in effect two muscles: a "sterno-cricoid" and a "crico-hyoid." There may or may not be a raphe present (figs. 4, 6, 10, 12) that bisects the muscle into anterior and posterior parts. If present, the raphe is unrelated to the attachment of the muscle to the posterior larynx.

OTHER EMBALLONUROIDS: In *Rhinopoma,* there is no attachment to the posterior laryngeal region. The sternohyoid is a reduced muscle that takes origin entirely from the anterior surface of the medial manubrium of the sternum. It begins posteriorly as a narrow, thin muscle. As it passes anteriorly, it narrows and thins even more. In all emballonurid genera except *Emballonura* and *Coleura,* the muscle is as described under "Origin" and "Insertion" above. In these two genera, there is one more unusual feature to this muscle. As it passes anteriorly from its origin on the sternum, it is deflected by and passes dorsal to the well-developed tracheal expansions that lie just posterior to the larynx. The muscle then passes ventrally to attach to the posterior larynx. Finally, it passes anteriorly from laryngeal attachment to insert ultimately on the basihyal. A more complete treatment of this unusual muscle may be found in Griffiths et al. (1991).

OTHER YINOCHIROPTERA: In megadermatids, the origin is entirely from the manubrium of the sternum, and the insertion is directly into the fibers of the geniohyoid and hyoglossus muscles (with a tendinous attachment to the basihyal—the "free-floating" condition). There is a prominent raphe that bisects the muscle (from which the sphincter colli takes

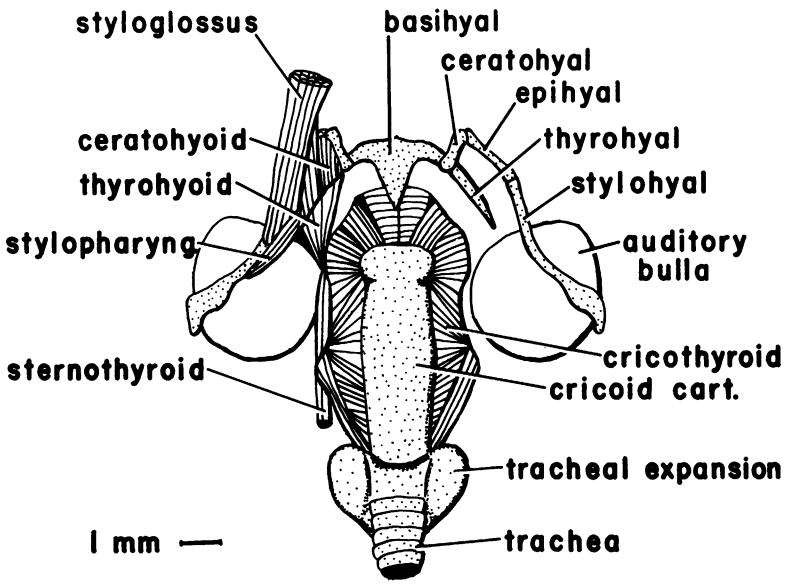

Fig. 15. Ventral view of the deep hyoid structures and the larynx of *Peropteryx kappleri.*

origin); anterior to this raphe the antimeres are fused. In nycterids and all rhinolophids, the origin is exclusively from the manubrium of the sternum, but otherwise the muscle is similar to the emballonurid condition.

COMMENTS: The attachment of the sternohyoid to the posterior larynx in all emballonurid bats is very unusual and may be unique among the Mammalia. Apparently, the shift of the origin of the omohyoid (see below) to the midpoint of the clavicle in both *Rhinopoma* and the Emballonuridae caused a duplication of function. The omohyoid paralleled the sternohyoid more closely and came to duplicate its function of hyoid/tongue retraction. Thus, the sternohyoid became superfluous, and (1) became reduced in *Rhinopoma* to a vestige of itself and (2) was freed in emballonurids to adopt a new function, that of extrinsic laryngeal muscle. This new function seems particularly well developed in *Emballonura, Coleura, Peropteryx,* and *Peronymus.*

M. sternothyroideus
Figures 1–15

ORIGIN: From the anterior surface of the medial head of the clavicle, just lateral and slightly dorsal to the origin of the lateral slip of the sternohyoid.

INSERTION: Onto the lateral surface of the thyroid cartilage.

OTHER EMBALLONUROIDS: This muscle is the same in all specimens dissected, except that in *Rhinopoma* the origin is broader. It originates from the lateral manubrium, from the sterno-clavicular articulation, and from the medial surface of the head of the clavicle.

OTHER YINOCHIROPTERA: This muscle is very reduced in all megadermatids, all nycterids, and in all rhinolophids except *Hipposideros armiger.* In all megadermatids and rhinolophids examined, it originates from the manubrium of the sternum only.

M. omohyoideus
Figures 1, 2, 4, 6, 8, 10, 12, 14

ORIGIN: From the anterior surface of the mid-clavicle.

INSERTION: By very short tendon onto the lateral basihyal bone, just lateral to the insertion of the sternohyoid.

OTHER EMBALLONUROIDS: This muscle is the same in all genera dissected. In all emballonurid genera, the anterior part of the omohyoid is fused with the anterior part of

the sternohyoid. The two muscles pass anteriorly as one to insert on the hyoid apparatus. There may or may not be a visible raphe that bisects the omohyoid.

OTHER YINOCHIROPTERA: In megadermatids, possibly because of the "free-floating" sternohyoid–omohyoid complex, this muscle has a very different insertion. The insertion is onto the posterior surface of the thyrohyal. In nycterids, the muscle is the same as in emballonurids. In rhinolophids, the muscle is completely absent, except in *Hipposideros diadema.* In *H. diadema,* the origin of this muscle is from the anterior surface of the scapula (not the clavicle).

COMMENTS: In virtually all other groups of mammals, the omohyoid takes origin from the scapula, usually from the anterior edge. In all bats dissected in this study except for the single species of rhinolophid bat where the muscle is present, the muscle has shifted its origin radically. Sprague (1943) reported an omohyoid with a scapular origin in the rhinolophids he dissected, and we can partially confirm his observation here.

M. thyrohyoideus
Figures 1–15

ORIGIN: From the lateral surface of the thyroid cartilage, just anterior to the insertion of the sternothyroid.

INSERTION: Onto the posterior surface of the thyrohyal element.

OTHER EMBALLONUROIDS: This muscle is the same in all emballonuroids dissected.

OTHER YINOCHIROPTERA: This muscle is the same in all Yinochiroptera.

DISCUSSION

In recent years, two differing hypotheses on the systematic relationships of genera within the family Emballonuridae have been proposed. Barghoorn (1977), using skull characters, tentatively suggested that the long-skulled, Old World genera *Taphozous* and *Saccolaimus* are most closely allied with the extinct genus *Vespertiliavus,* and that together they compose a clade within the family Emballonuridae. He further suggested that the shorter-skulled Old World genera, *Emballonura* and *Coleura,* are more closely related to the New World emballonurids, forming with them a second major clade within the family. Within the second clade, *Emballonura* forms a monotypic basal line, and the remaining genera form a clade in which there are two major subgroups. The genera *Cormura, Centronycteris, Saccopteryx, Diclidurus, Cyttarops,* and *Depanycteris* form one group. The genera *Peropteryx, Peronymus, Balantiopteryx,* and the Old World *Coleura* form the second. Two surprising features of the second group are (1) the presence of *Coleura* among the New World genera and (2) that *Peronymus* is more closely related to *Balantiopteryx* than to *Peropteryx.*

Robbins and Sarich (1988) proposed a different phylogeny based on immunological and electrophoretic data. They agreed with Barghoorn (1977) that *Taphozous* and *Saccolaimus* form a basal clade within the Emballonuridae, with all other genera forming a second clade. However, within the second clade, the Old World genera *Coleura* and *Emballonura* form a clade, while all New World genera form a second clade that contains an unresolved hexachotomy. On one of the six lines of the hexachotomy, *Peropteryx* and *Peronymus* are depicted as phylogenetically close, with *Cormura* a slightly more distant genus on the same line. Robbins and Sarich's (1988) phylogeny differs from Barghoorn's in the placement of *Coleura* with *Emballonura,* and in the close relationship proposed for the genera *Cormura, Peropteryx,* and *Peronymus.*

Apomorphic character states of the emballonurid and rhinopomatid hyoid regions are listed in table 1, and the cladogram derived from these data is shown in figure 16. There is a basal clade, composed of *Taphozous* and *Saccolaimus,* which is a sister group of all other emballonurids. Within the remaining emballonurids there are two clades: one comprising *Emballonura, Coleura,* and *Mosia,* and the other comprising all the New World genera. Up to this point, our hyoid data cladogram agrees strongly with the protein data cladogram generated by Robbins and Sarich (1988), with the exception of the inclusion of the genus *Mosia,* which Robbins and Sarich did not mention. *Mosia* is a recently resurrected, monotypic genus containing the species *M. nigrescens,* which has hitherto been considered part of the genus

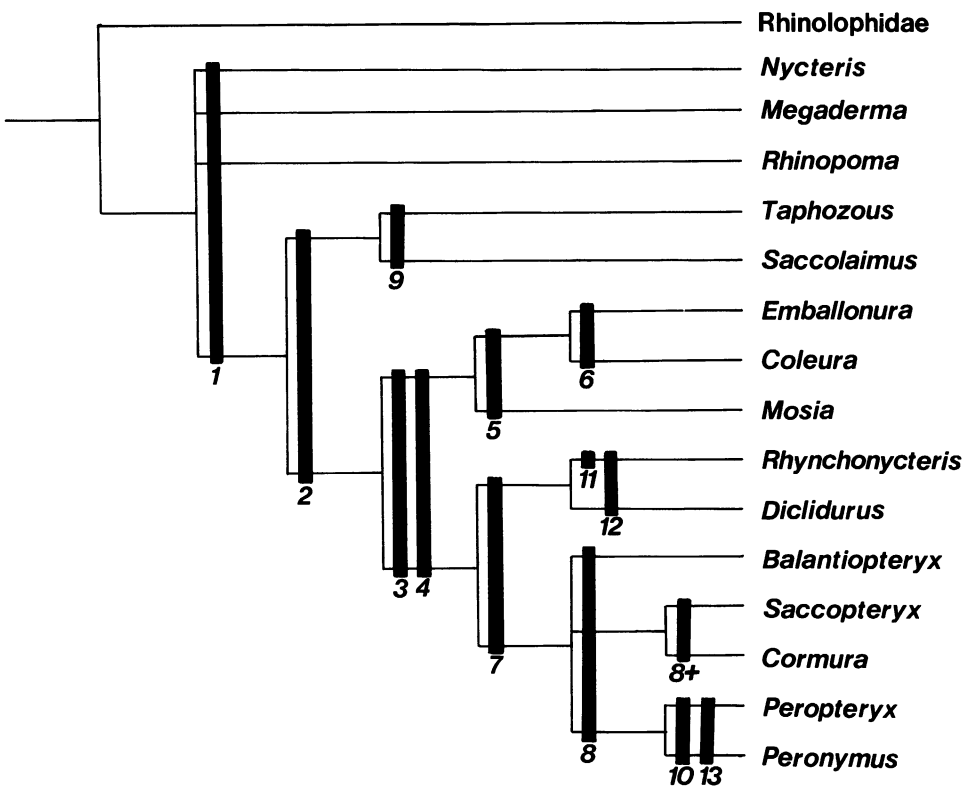

Fig. 16. Cladogram showing relationships among genera examined in this study. Numbers refer to character states in table 1. A "+" next to a number refers to a strong expression of the trait in table 1.

Emballonura. The hyoid data most strongly support the close relationship between species of *Coleura* and species of *Emballonura*, excluding only *nigrescens*. Griffiths et al. (1991) have thoroughly explored this question and have concluded that it is appropriate to resurrect Gray's (1843) genus *Mosia*, and to place *nigrescens* in the genus. Although initially it might seem a minor point of disagreement over terminology, the disagreement actually runs deeper than this. Robbins and Sarich (1988) did examine *nigrescens* (as the genus *Emballonura*), and most of their data suggest that *nigrescens* is more closely related to other *Emballonura* than to *Coleura*. However, some electrophoretic data from Robbins's doctoral dissertation (Robbins, 1983) support the hypothesis that *nigrescens* is a sister taxon of a group containing the remaining *Emballonura* species and *Coleura* (Robbins, personal commun.). Thus, the hyoid data and some of the protein data directly contradict other protein data on this point. More work using different data sets will undoubtedly shed light on this question and should help to resolve the disagreement.

Within the New World clade, the hyoid data suggest that there are two clades: one containing *Rhynchonycteris* and *Diclidurus*; the other containing *Balantiopteryx, Saccopteryx, Cormura, Peropteryx,* and *Peronymus*. Within the latter clade, there is evidence supporting a close relationship between *Saccopteryx* and *Cormura*, and very strong evidence supporting a close relationship between *Peropteryx* and *Peronymus*. Although this clade in our figure 16 and in Robbins and Sarich's (1988) cladogram initially look very different, in fact there is only one area where the two disagree: whether *Cormura* is more closely related to *Saccopteryx* (as the hyoid data suggest) or to *Peropteryx* and *Peronymus* (as the

TABLE 1

Summary of Apomorphies Used in Constructing the Cladogram (fig. 16)

(+ = apomorphic character state; − = plesiomorphic character state; ++ = strong expression of the apomorphy)

Character state	Taxon[a]												
	Rhi	Tap	Sal	Emb	Col	Mos	Rhy	Dic	Bal	Sap	Cor	Pep	Pen
1. Omohy. origin shift to clav.	+	+	+	+	+	+	+	+	+	+	+	+	+
2. Sternohy. attach. to larynx	−	+	+	+	+	+	+	+	+	+	+	+	+
3. Reduction and fusion of geniohy.	−	−	−	+	+	+	+	+	+	+	+	+	+
4. Some reduction of jugulohy.	−	−	−	+	+	+	+	+	+	+	+	+	+
5. Extended insert. of ceratohy.	−	−	−	+	+	+	−	−	−	−	−	−	−
6. Deflect. of sternohy. dorsally	−	−	−	+	+	−	−	−	−	−	−	−	−
7. Loss of jugulohy.	−	−	−	−	−	−	−	+	+	+	+	+	+
8. Elong. basihyal and separ. of hyogl.	−	−	−	−	−	−	−	−	+	++	++	+	+
9. Loss of stylohy.	−	+	+	−	−	−	−	−	−	−	−	−	−
10. Peculiar attach. sternohy. to larynx	−	−	−	−	−	−	−	−	−	−	−	+	+
11. Extended origin of cricothy.	−	−	−	−	−	−	+	−	−	−	−	−	−
12. No insert. of mylohy. on thyrohyal	−	−	−	−	−	−	+	+	−	−	−	−	−
13. Stylohy. insertion on basihyal	−	−	−	−	−	−	−	−	−	−	−	+	+

[a] Abbreviations of taxa: Rhi, *Rhinopoma*; Tap, *Taphozous*; Sal, *Saccolaimus*; Emb, *Emballonura*; Col, *Coleura*; Mos, *Mosia*; Rhy, *Rhynchonycteris*; Dic, *Diclidurus*; Bal, *Balantiopteryx*; Sap, *Saccopteryx*; Cor, *Cormura*; Pep, *Peropteryx*; and Pen, *Peronymus*.

protein data suggest). All other apparent differences are due to the greater resolution provided by the hyoid data.

On the other hand, the hyoid cladogram is very different from the cladogram based on cranial characters (Barghoorn, 1977). In particular, some of the strongest hyoid evidence (i.e., in our opinion, least likely to be undetected homoplasies) suggests there is a close relationship between *Coleura* and non-*nigrescens* species of *Emballonura,* and between *Peropteryx* and *Peronymus.* Barghoorn's (1977) conclusions differ. We cannot agree that *Coleura* belongs with the New World genera, and our groupings of genera within the New World clade are different from his.

In sum, it is interesting that the hyoid data support and add to the conclusions reached by Robbins and Sarich (1988). New data should resolve the two relatively minor areas of disagreement: (1) how *Cormura* is related to other New World emballonurids and (2) how *Coleura, Emballonura,* and *Mosia* are arranged within their clade.

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Aspects of the Morphology of the Cochlea in Microchiropteran Bats: An Investigation of Character Transformation

MICHAEL J. NOVACEK[1]

ABSTRACT

Comparative study of the cochlea in 95 species of microchiropteran bats can be related to theories for the origin of special cochlear features that distinguish the group. Most microchiropteran species show weak petrosal ossification, yielding a condition where the cochlear labyrinth is clearly visible externally (the phanerocochlear state). Some microchiropterans, however, show a thicker encasement of petrosal bone around a "cryptic" cochlea, a condition similar to that in megachiropterans and other mammals (the cryptocochlear state). Comparisons of adult structure, allometric relations, structural and functional correlates, and inferred ontogenies and phylogenies suggest that an ontogeny producing the phanerocochlear condition was ancestral for microchiropterans. This unique ontogeny represents a mosaic of paedomorphic patterns involving arrested ossification of the petrosal and peramorphic trends involving pronounced expansion and increased torsion of the cochlea. The arrested ossification is viewed as an accommodation to the problem of "packing" middle ear structures in a space constrained by the expanded cochlea. The occurrence of the cryptocochlear condition shows plasticity, particularly among larger microchiropterans, where I argue that packing problems are less severe. The unusual expansion of the microchiropteran cochlea can be related to increase in basilar membrane length. The latter parameter probably relates to increased sensitivity to a spectrum of echolocation signals.

INTRODUCTION

The unique capabilities of microchiropteran bats for time-structured echolocation (Fenton, 1984) have been tied to the unusual architecture of the auditory system in these animals. Notable aspects of this system include the cochlea and its relationship to surrounding basicranial elements. In microchiropterans, the relatively large cochlea (Stanek, 1933; Novacek, 1985a), which houses the membranous and bony labyrinth of the inner ear, is often only thinly covered by petrosal bone (fig. 1B). In this "phanerocochlear" condition, the osseous labyrinth is well exposed, lending to the cochlea the snaillike appearance (fig. 1B) suggested by its name. Another feature attributed to microchiropterans is the very weak articulation of the cochlea with surrounding basicranial elements; connections are effected only by thin splints of bone between large fissures in the tympanic roof (fig. 1B), a condition thought to function in reducing bone conduction of laryngeal vibrations (Henson, 1970). The enlarged, "acoustically isolated" cochlea has been suggested by some authors to be a feature present in the common ancestor of all Microchiroptera (Van Valen, 1979: 112) as part of the nexus of traits that emerged with the origin of a very specialized mode of echolocation (Henson, 1970).

These correlates among structure, function, and phylogeny, however evocative, entail some difficulties. Discussions of the function of cochlear structure are not heavily

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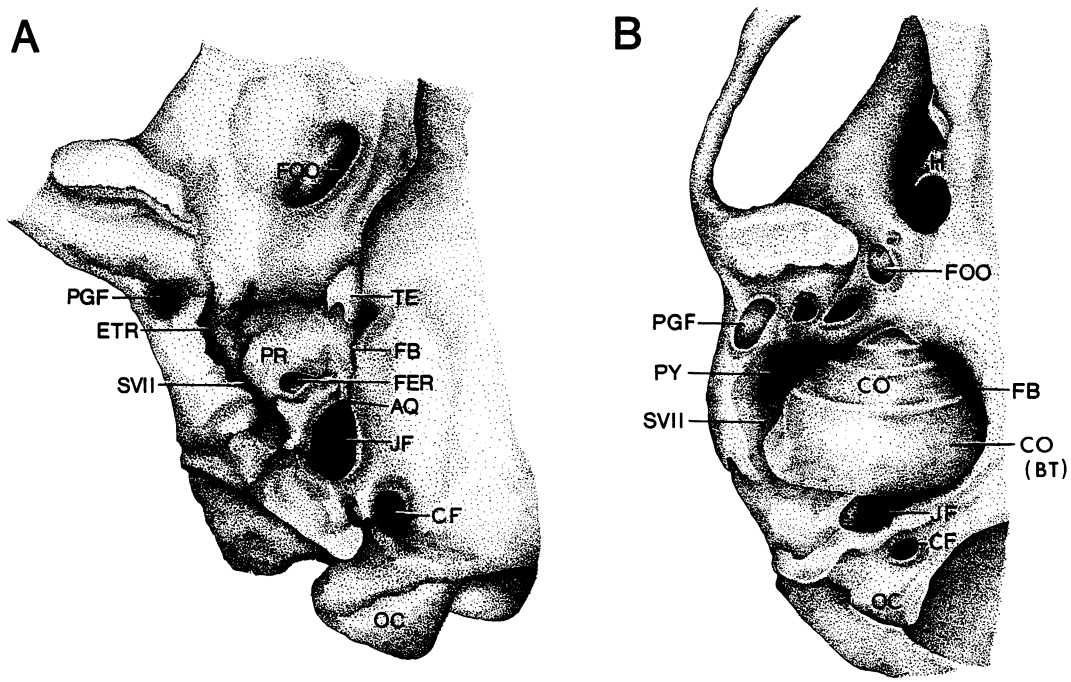

Fig. 1. Right basicrania of (**A**) *Pteropus poliocephalus,* SDSU 1152, and (**B**) *Rhinolophus* sp., SDSU 1215. Both specimens with bulla, ectotympanic, and ear ossicles removed. Not to scale. Symbols: AQ, aqueductus cochleae; CF, condyloid foramen; CO, cochlea; CO (BT), basal turn of cochlea; ETR, epitympanic recess; FB, basicochlear fissure; FER, fenestra rotundum; FOO, foramen ovale; H, hamular process; JF, jugular foramen; OC, occipital condyle; PGF, postglenoid foramen; PR, promontorium cochleae; PY, pyriform fenestra; SVII, sulcus for facial (VII) nerve; TE, flange for eustachian tube (rostral entotympanic).

anchored by experimental evidence. Moreover, the structural variation of the microchiropteran cochlea is more pronounced than is often suggested in published treatments. For example, Stanek's (1933) profusely illustrated masterwork on the bat otic region was restricted to genera in three families (Rhinolophidae, Vespertilionidae, and Natalidae), where the cochlear spirals (or turns) are clearly exposed and the cochlea is weakly joined to other elements. Some other microchiropterans, however, show a much thicker ossification of the petrosal that obscures the labyrinthine structure of the cochlea (fig. 2B). In many cases, this "cryptocochlear" condition is associated with more extensive articulation between the cochlea and adjacent basicranial elements. Such features resemble the condition found in megachiropteran bats (fig. 1A) and also resemble conditions in most other groups of mammals.

These simple comparative observations give rise to an interesting dilemma. Is the phaneric, semi-isolated cochlea most often tied to the echolocating system in microchiropterans indeed ancestral for the group? If not, this striking architecture must have arisen independently two or more times within the suborder, presumably after some form of time-structured echolocation was acquired in microchiropterans. This unexpected but quite feasible scenario hinges on an argument of homology, namely that the more cryptic cochlea shown in figure 2B is simply a retention of the primitive mammalian condition. Herein, I argue that the cryptocochlear condition in microchiropterans is not strictly a retention of the more primitive trait. Rather, it is more likely a secondary modification of an ontogeny that generally gives rise to the phaneric, semi-isolated cochlea in most adult microchiropterans. The argument is devel-

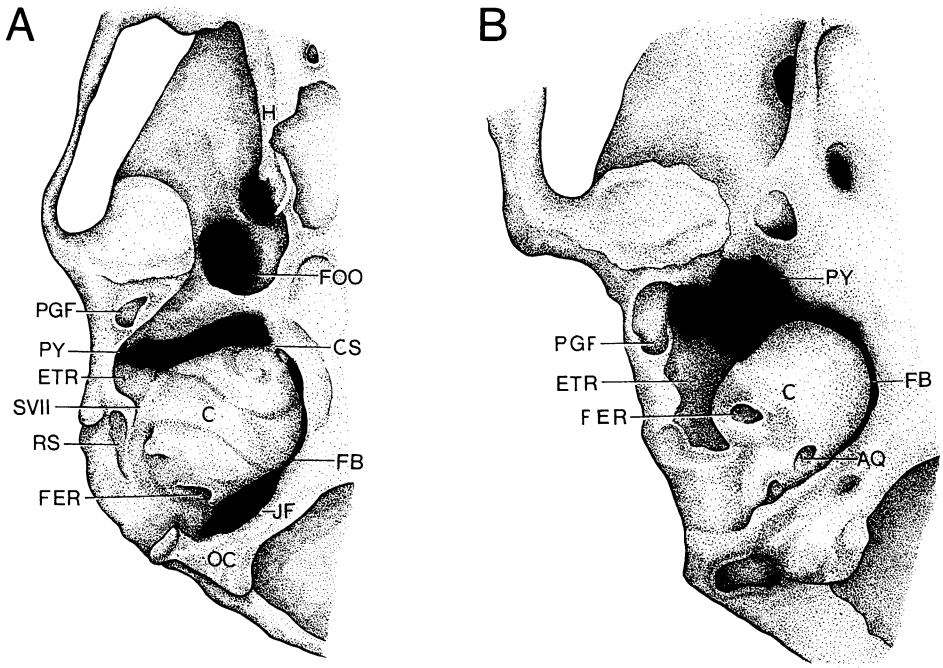

Fig. 2. Right basicrania of (**A**) *Natalus* sp., SDSU 780, and (**B**) *Nycteris* sp. (probably *N. grandis*), SDSU 1205. Not to scale. CS, cochlear–sphenoid "bridge"; RS, recess for the origin of the stapedius muscle. All other symbols as in figure 1.

oped from a survey of cochlear features and some consideration of what is known of bat function, ontogeny, and phylogeny.

This argument does not strictly require that megachiropterans and microchiropterans are monophyletic, although bat monophyly is assumed here. Proposals for the diphyletic origin of bats (e.g., Smith and Madkour, 1980; Pettigrew, 1986) are addressed and rejected elsewhere (Wible and Novacek, 1988). For a response to a lengthy version of the diphyletic argument (Pettigrew et al., 1989) see Baker et al. (1991).

Acknowledgments

It is an honor to contribute to a volume dedicated to Karl Koopman, whose extraordinary knowledge of mammal diversity and evolution inspired my work on this and other problems. In addition to providing access and guidance to the AMNH collection of bats, Dr. Koopman shared many helpful insights. He also coined the terms phanerocochlear and cryptocochlear as used here. I thank Nancy Simmons, Ross MacPhee, Gary Morgan, Tom Griffiths, Chris Beard, Malcolm McKenna, and Mark Norell for critical reviews of the manuscript. Dr. G. Petter at the Museum National d'Histoire Naturelle, Paris, allowed study of the Myzopodidae. Dr. J. E. Hill permitted study of the rare collection of Craseonycteridae at the British Museum of Natural History.

COMPARATIVE ANATOMY

Variations in three features of cochlear structure were examined: (1) the relative size of the cochlea, with particular reference to the size of the basal turn; (2) the presence of either the phanerocochlear or cryptocochlear condition in the adult skull; and (3) the degree of isolation of the cochlea from surrounding basicranial elements. Aspects relating to these features (e.g., the osseous contacts between the cochlea and the basioccipital) are mentioned where appropriate. Specimens representing 102 species from all 17 Recent bat families were examined. Fossils of the Eocene

genera *Icaronycteris* and *Palaeochiropteryx* were also studied. Material studied is housed in the Mammalogy Department of The American Museum of Natural History (AMNH) and the mammalogy collections at San Diego State University (SDSU); the Yale Peabody Museum (YPM); the Senckenberg Naturmuseum und Forschungsinstitut, Frankfurt (SMF-ME); the Museum National d'Histoire Naturelle, Paris (MNHN); and the British Museum of Natural History, London (BMNH).

COCHLEAR SIZE: Quantitative study shows that microchiropterans are remarkable for having a greatly expanded cochlea. The feature is universal for the suborder and is found even in the earliest known bats, the Eocene microchiropterans *Palaeochiropteryx* and *Icaronycteris* (Novacek, 1985a, 1987: fig. 6). One aspect of cochlear size, maximum cochlear width, is particularly revealing. The hypertrophy of the cochlea seems to be primarily a function of expansion of the basal turn (fig. 1B). This is of interest because the frequency spectrum of the receptor neurons in the labyrinth decreases from the basal to the apical regions. Accordingly, the basal turn is a region of high-frequency reception applicable to ultrasonic echolocation (Henson, 1970; Dallos, 1973; Bruns, 1979; Bruns et al., 1983–84). The maximum width of the cochlea corresponds to the width of the basal turn.

A plot of maximum cochlear width against skull length demonstrates the ubiquity of the hypertrophied cochlea in Microchiroptera (fig. 3). The convex polygons define the outer boundaries of a cluster of points for each of the two bat suborders. The polygon for 69 species (in 63 genera) of Microchiroptera representing 14 of the 16 Recent families (Craseonycteridae and Myzopodidae were not available for dissection and measurement, but qualitative observations would predict their placement within the microchiropteran polygon), as well as two species of Eocene fossil bats, does not overlap with a polygon enclosing 26 species (in 26 genera) of Megachiroptera (fig. 3). In other words, the cochlear width is always greater for a microchiropteran than for a megachiropteran of corresponding skull size. This pattern also holds for comparisons between microchiropterans and lipotyphlans, macroscelideans, and a variety of other small mammals (Novacek and Graybeal, in prep.).

Other differences between the bat suborders with respect to these parameters are noteworthy. In Megachiroptera and Lipotyphla, cochlear width shows both a high correlation and low positive allometry against skull length. In Megachiroptera, for example, the correlation coefficient (r) is 0.92 and the slope is 0.30. In Microchiroptera there is a much weaker correlation ($r = 0.64$) and a much higher positive allometry (slope = 0.80) for cochlear width versus skull length (Novacek, 1985a, 1987). Hence, the marked expansion of the cochlea in various microchiropteran species is poorly scaled against one parameter of skull size, and other factors—perhaps sensory modes and related behaviors—may influence these trends.

A series of statistical tests of the above results demonstrates that there is no significant variation in cochlear size within selected species (Novacek and Graybeal, in prep.). Cochlear size, however, shows marked intertaxon differences and may vary to an extraordinary degree among species of the same microchiropteran genus (Henson, 1970). Functional reasons for this variation are poorly understood. Nonetheless, the large size and the peculiar allometric relationships of the cochlea in microchiropterans serve well to distinguish this group from other mammals, and these features suggest a system well suited for perceiving complex echolocation signals (Henson, 1970; Bruns et al., 1983–84; and remarks below).

PHANERIC OR CRYPTIC COCHLEA: With reference to the phanerocochlear condition, Henson (1970: 209) stated: "Although the cochlea of Chiroptera [Microchiroptera] is composed of very dense bone . . . it lacks the extensive deposition of bone found in higher mammals. In adult bats [microchiropterans] the cochlea closely resembles the cartilaginous model seen in the embryo; it is similar to the otic capsule of higher forms. How much of the bat's inner ear constitutes otic capsule and how much is added petrosal bone is not known. In many small species, such as *Natalus* . . . the only bone, other than that immediately surrounding the cochlea, is the bone which forms part of the fossa for the stapedius

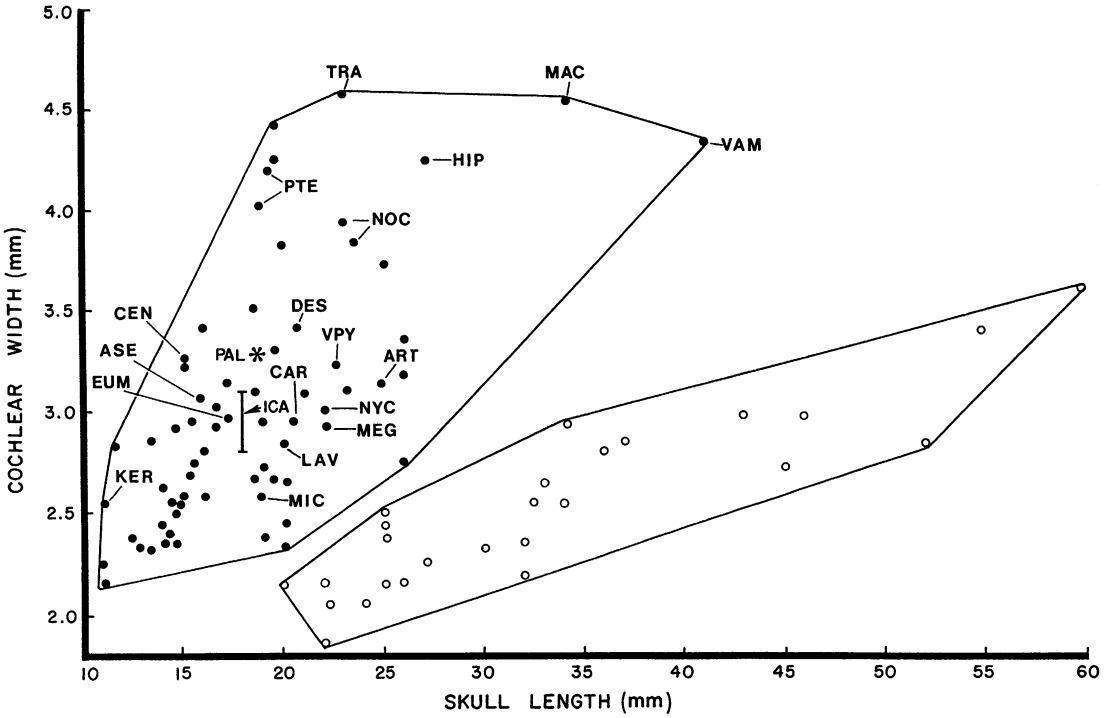

Fig. 3. Plot of maximum cochlear width against skull length for 69 species of Microchiroptera (solid circles) and 26 species of Megachiroptera. Some points represent two taxa with nearly identical plots. Symbols and acronyms represent the Eocene bat taxa: ICA, *Icaronycteris index* (vertical line showing range of error); PAL, *Palaeochiropteryx tupaiodon* (asterisk). Acronyms are also given for species measured that show the cryptocochlear condition: ART, *Artibeus planirostris*; ASE, *Asellia tridens*; CAR, *Cardioderma cor*; CEN, *Centurio senex*; DES, *Desmodus* sp.; EUM, *Eumops bonariensis*; HIP, *Hipposideros diadema*; KER, *Kerivoula hardwicki*; LAV, *Lavia frons*; MAC, *Macroderma gigas*; MEG, *Megaderma spasma*; MIC, *Micronycteris brachyotis*; NOC, *Noctilio leporinus*; NYC, *Nycteris grandis*; PTE, *Pteronotus parnellii*; TRA, *Trachops cirrhosus*; VAM, *Vampyrum spectrum*; VPY, *Vampyrops lineatus*. Modified from Novacek (1987).

muscle and part of the facial canal [the mastoid and epitympanic portions of the petrosal]." Although one might object to the above-quoted distinction between otic capsule and petrosal bone, an essential point is hardly contestable—the cochlea in adult microchiropterans shows an intriguing similarity to the embryonic otic capsule in mammals generally. Moreover, the lack of extensive deposition of bone around the cochlea is characteristic of the great majority of microchiropteran higher groups. Bone is so thin in this region that the labyrinthine structure of the cochlea is clearly visible externally in Emballonuridae, Rhinopomatidae, Craseonycteridae, Myzopodidae, Furipteridae, Natalidae, Thyropteridae, Molossidae (except in larger species of *Eumops*), and Mystacinidae. The condition is also present (but not universal) in Rhinolophidae (fig. 1B), Nycteridae, Vespertilionidae, Mormoopidae, and Phyllostomidae. Hence, the phanerocochlear condition is constant in nine families and variably present in five additional families of Microchiroptera. Although it cannot be established with certainty, the cochlea in the early Eocene microchiropteran *Palaeochiropteryx* also appears to be phaneric, as radiographs (fig. 4 in Novacek, 1987) show relatively thin bone deposition in this region that contrasts with the condition seen in radiographs of extant taxa with the cryptocochlear condition (cf. *Pteronotus* (*Phyllodia*) *parnellii*; fig. 13C in Henson, 1970).

The cochlea in the Eocene *Icaronycteris* is not sufficiently preserved to allow an account of its detailed structure.

The less widespread cryptocochlear condition does characterize at least two familial-level taxa, the Megadermatidae and the Noctilionidae. The condition is also seen in the nycterid *Nycteris grandis* (but not *N. hispida*), the hipposiderine rhinolophids (e.g., *Hipposideros* [variable] and *Asellia*), the vespertilionid *Kerivoula,* the mormoopid *Pteronotus* (*Phyllodia*) *parnellii* (but not *P. personatus* and *P. davyi*), and several members of the diverse Phyllostomidae, particularly the larger phyllostomintes (e.g., *Vampyrum, Trachops*).

Several aspects of this distribution are relevant. It is obvious that the cryptocochlear condition is not widespread among families of Microchiroptera. Moreover, its occurrence, as summarized above, can vary even among species within a genus. The extreme case of variation was observed within the species *Eumops bonariensis,* where a few larger individuals showed a slightly cryptic condition in contrast to the phaneric condition seen in most individuals of this species and all other molossids studied.

It is also noteworthy that the cryptocochlear condition is more characteristic of larger species (fig. 3). *Noctilio* and megadermatids are large bats, as are most of the other cryptocochlear species mentioned above. This trait is seen in larger phyllostomids, larger hipposiderines, and larger species of *Nycteris* (fig. 2B). In fact, nearly all the species showing this condition fall within the upper section of the polygon for relative cochlear width versus skull length (fig. 3). This does not preclude cases where larger bats have phaneric cochleas (e.g., *Rhinolophus*). Nonetheless, the cryptocochlear condition is rare in microchiropteran species with skull lengths less than 20 mm and is virtually absent in the species with skull lengths under 15 mm (fig. 3). The only exception observed in this study is the vespertilionid *Kerivoula* (skull length = 11.58 mm), where the presence of the cryptic cochlea is a distinct departure from the usual condition in the family.

These comparisons are generally clear-cut, and the contrast between the crypto- and phanerocochlear conditions is readily apparent (e.g., figs. 1, 2). There are, however, cases showing a spectrum of conditions somewhere between the two extremes. This problem is most evident in the phyllostomids, where some genera (e.g., *Sturnira, Lonchophylla, Glossophaga*) show a thicker petrosal but not to the extent that the labyrinth is completely obscured. As noted above, such intermediate states also occur among individuals of *Eumops bonariensis.* Perhaps relevant here is the observation that the cryptocochlear condition is often associated with cases where not just the petrosal but the skull as a whole shows a greater degree of ossification. This suggests that subtle differences in ontogeny might give rise to either crypto- or phanerocochlear conditions or to a range of intermediate states.

COCHLEAR ISOLATION: In microchiropterans the cochlea is not generally tightly articulated with surrounding basicranial elements. Attachments are usually formed craniomedially—between the cochlea and the sphenoid complex in the region of the eustachian tube—and posterolaterally—via the petromastoid flange in the region of the sulci for the facial (VII) nerve and the fossa for the stapedius muscle (figs. 1B, 2). Between these attachments are large spaces that house a variety of connective tissues, nerves, and blood vessels. These spaces are the anterolateral pyriform fenestra (PY), the anteromedial to medial basicochlear fissure (FB), and the posteromedial jugular foramen (JF). The size of these spaces varies in bats. Although FB and JF are present in megachiropterans, they are rarely broadly confluent, and PY is absent (fig. 1A). In these bats, the cochlea is encased in the thick petrosal bone exposed ventrally as the promontorium, and is well attached to the surrounding basicranium (fig. 1A). PY is developed in some mammalian groups, most notably the soricoid lipotyphlans. One might conclude that because this opening conceivably represents an incipient stage of ossification in the tympanic roof, its persistence in adults is merely primitive. The absence of PY, however, in adult skulls of the majority of archaic mammalian taxa, as well as representative marsupials and eutherians, suggests that the primitive ontogeny for eutherians carried ossification to a stage where the tympanic roof was largely occupied by bone.

The persistence of PY in adult skulls therefore seems a specialized condition in the groups where it occurs.

It is important to note that most microchiropteran species show development of PY, FB, and JF to an extent greater than outside this group. In some cases, these openings are very large and FB and JF coalesce (figs. 1B, 2a). The openings are generally less developed in Myzopodidae, Furipteridae (where PY is, however, large), Thyropteridae, Mormoopidae, some hipposiderine Rhinolophidae (e.g., *Asellia*), Megadermatidae, Emballonuridae, and Rhinopomatidae. Extensive development and confluence of these openings—and thus isolation of the cochlea—are most extreme in rhinolophines (fig. 1B), natalids (fig. 2A), noctilionids, some phyllostomids, and nycterids (fig. 2B).

The weak basicranial attachment of the cochlea in microchiropterans is often associated with the phanerocochlear condition (figs. 1B, 2A). Conversely, in some taxa (*Asellia,* megadermatids) the cochlea is both cryptic and less isolated from the surrounding basicranial elements. The two conditions are, however, far from strongly correlated. Cochlear isolation is notable even in cases where bone deposition is thicker and more extensive, and the cochlea does not appear externally as a labyrinthine structure (e.g., *Nycteris* [fig. 2B], *Noctilio*). Some degree of cochlear isolation may be a signature of microchiropterans (Van Valen, 1979), but the variation in this condition does not clearly correlate with other aspects of otic structure described here.

STRUCTURAL AND FUNCTIONAL CORRELATES

The above comparisons can be considered in light of theories concerning the size and structure of the microchiropteran cochlea in relation to function and adaptation. These theories are not based to any extent on experimental evidence. They are largely an exercise in correlating a known structure to a known set of physiological parameters or behaviors in one or more species. In mammals, cochlear size has been related to parameters that include the radius of the turns of the labyrinth, the number of turns, and the amount of bone accretion during ontogeny. The first two of these parameters may be considered in relation to other aspects of cochlear architecture, such as the total number of cochlear neurons and the length of the basilar membrane lining the cochlear duct. Bruns et al. (1983–84) observed that the basilar membrane of microchiropterans does not differ significantly in form from that of selected other small mammals (shrews, mice, rats) showing the generalized sensory behavior that emphasizes high-frequency reception (Fleischer, 1973). Although most microchiropterans measured showed a significantly greater length of the basilar membrane, certain species (e.g., *Myotis lucifugus*) showed lengths comparable to the basilar membrane length in *Mus musculus* (Bruns et al., 1983–84).

It should be noted that the measurements of basilar membrane length in Bruns et al. (1983–84) for *Mus, Crocidura,* and 10 species of microchiropterans were provided without reference to cochlear or skull dimensions. For example, similarities in basal membrane length between *Mus musculus* and *Myotis lucifugus* may be misleading, as skull size in the former species is significantly greater than in the latter. Moreover, some mammals (e.g., megachiropterans) show high correlations between skull length or width and cochlear dimensions (fig. 3). A preliminary analysis of specimens representing 9 of the 10 bat species listed by Bruns et al. (1983–84) (*Taphozous nudiventris* was not available for measurement) showed a strong relationship between maximum cochlear width and basilar membrane length, with a correlation coefficient of 0.89 (fig. 4). By contrast, there was essentially no correlation between skull length and cochlear width ($r = 0.15$), or skull length and basilar membrane length ($r = 0.10$). This result seemed largely influenced by the fact that the cochlea is aberrantly small in *Megaderma lyra.* Removal of this species produced a correlation coefficient of 0.79 between skull length and cochlear width for the remaining eight species. Nonetheless, a larger sampling of microchiropteran species revealed much weaker correlations between these parameters ($r = 0.64$) than in megachiropterans ($r =$

0.92) and lipotyphlan insectivorans (fig. 3; Novacek, 1985a, 1987; Novacek and Graybeal, in prep.).

This preliminary analysis suggests that for nine microchiropteran species various cochlear dimensions are not strongly correlated with skull size, but the diameter of the basal turn is a very good predictor of basilar membrane length. The latter correlation suggests an emphasis on expansion of the neural region for reception and discrimination of a richer variety of higher frequency signals. In this regard, Bruns et al. (1983–84) cited experimental evidence to suggest that elongation of the basilar membrane is related to expanded representation of echolocation sounds on the basilar membrane. For example, *Megaderma lyra,* the species in the sample with the shortest basilar membrane length, has a relatively primitive short multiharmonic echolocation signal (Simmons and Stein, 1980). This species also uses passive acoustic localization as well as echolocation to apprehend prey (Fiedler, 1979). The scarcity of data on basilar membrane length outside of this small sample of microchiropterans precludes broader inference.

Basilar membrane length is also likely to be correlated with the number of cochlear turns, although quantitative data are lacking. A range of between 2.5 and 3.5 turns is known for microchiropterans (Pye, 1967), and this significantly exceeds the number of turns found in the most conservative condition within Megachiroptera (e.g., 1.75 turns in species of *Pteropus*). There is notable variation in the number of cochlear turns in microchiropterans, and the pattern does not show any obvious trends or functional implications (Henson, 1970).

A component of cochlear design that does clearly distinguish microchiropterans is the number of afferent neurons of the spiral ganglion. Small mammals (e.g., shrews and rodents) have between 5200 and 6900 cochlear neurons, whereas species representing nine families of microchiropterans vary between 13,400 in *Hipposideros fulvus* and 55,300 in *Myotis lucifugus* (Bruns et al., 1983–84). Whereas counts are highest in the middle region of the cochlea for "reference" mammals (mouse, guinea pig, cat, man), microchiropterans exhibit highest innervation in the basal and middle regions, where echolocation frequencies are perceived (Bruns and Schmieszek, 1980; Bruns et al., 1983–84). One might conjecture that hypertrophy of the basal region of the microchiropteran cochlea is related to the proliferation of cochlear neurons. Measurements of representative specimens in 9 of the 10 species assessed for neuronal traits by Bruns et al. (1983–84) show essentially no correlation between neuronal population size and cochlear width ($r = 0.15$) or basilar membrane length ($r = 0.09$). In fact, counts are highest (55,300) in *Myotis lucifugus* (Ramprashad et al., 1978, 1979), the species in the sample with the shortest basilar membrane and the smallest cochlea (the relationship for all nine species measured is not, however, an inverse one). Thus, there is only contradictory evidence that hypertrophy of the basal cochlea and increase in length of the basilar membrane represent a volumetric accommodation to increased sensory innervation. High neuronal counts seem more a function of much greater neuronal density

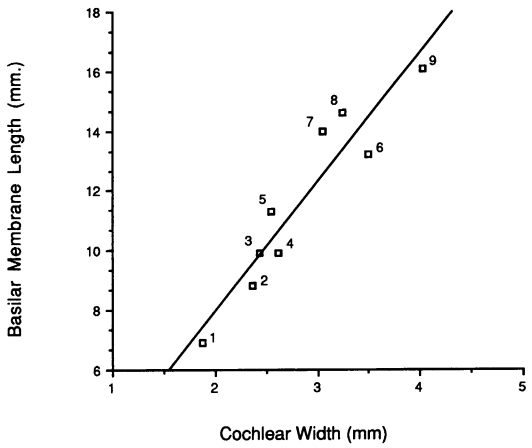

Fig. 4. Relationship of cochlear width (equivalent to diameter of the basal turn) and basilar membrane length in nine species of Microchiroptera. y-intercept = −0.72; slope = 4.30; correlation coefficient (r) = 0.89. Taxa: 1, *Myotis lucifugus*; 2, *Hipposideros fulvus*; 3, *Megaderma lyra*; 4, *Hipposideros speoris*; 5, *Rhinopoma hardwicki*; 6, *Pteronotus parnellii*; 7, *Noctilio albiventris*; 8, *Molossus ater*; 9, *Rhinolophus ferrumequinum.* Basilar membrane data are from Bruns et al. (1983–84).

than a function of increased length of the basilar membrane or cochlear volume.

Referring to the possible function of greater neuronal density, Bruns et al. (1983–84) suggested: "An increased number of cochlear neurons is proposed to improve the echolocation signals of bats. . . . In addition there might be a correlation between the number of neurons and the bandwidths of the frequency modulated signals. *Myotis lucifugus* emitting exclusively very broad banded signals has the highest number of neurons." Moreover, there is experimental evidence that very high regional densities for neurons are matched with very focused reception ("the acoustic fovea") of a given frequency band, which in some species (e.g., *Rhinolophus ferrumequinum*) provides a means to detect very small modulations produced by the wing beats of prey insects (reviewed in Neuweiler et al., 1980). These data suggest that while both increase in basilar membrane length and greater density of cochlear neurons may be associated with highly developed ultrasonic echolocation, these parameters are linked independently with various sensory adaptations.

With reference to the phanerocochlear condition itself, little in the way of function has been suggested. As noted above, most discussions of this feature simply mention its existence and comment on its "embryonic" quality. There is no apparent reason why such a thinly covered otic capsule should be particularly advantageous to echolocating bats. The feature, however, does seem more readily explainable as an integral aspect of a unique ontogeny for the microchiropteran auditory system (Novacek, 1985b).

The marked isolation of the cochlea from surrounding elements supposedly relates to special hearing adaptations in microchiropterans. Henson (1970) suggested that this condition may serve to attenuate bone conduction created by laryngeal vibrations during vocalizations. Normally, some attenuation would be facilitated by the dense bone encasing the cochlear labyrinth. In cases where such deposition is minimal, isolation of the cochlea from surrounding bones might be advantageous. In this regard, it is noteworthy that the basicranial fissures separating the cochlea from other bones are filled with large venous sinuses, extensive depositions of fat, and a peculiar type of connective tissue (Henson, 1961). Of note here is the fact that in certain taxa (e.g., *Cheiromeles, Pizonyx*) where the lateral and posterior semicircular canals are proximal to the squamosal and occipital, respectively, the latter bones are very thin and fibrous and a defect or opening occurs on the lateral surface of the skull (Henson, 1970). There thus seems a priority for the isolation of the inner ear and vestibular system, even at the cost of weakening the cranial vault. The condition found, however, in certain species (e.g., *Pteronotus* (*Phyllodia*) *parnellii*), where the very large aqueductus cochleae and the perilymphatic space are essentially in contact with cerebrospinal fluid, argues against this view. In such cases, it seems that any vibrations affecting the skull bones would be readily transmitted to the cochlear fluids (Henson, 1970).

ONTOGENY AND PHYLOGENY

The above considerations do not account for other factors that may greatly influence cochlear size and structure. These are the ontogenies that control modifications of interrelated components, and the history of descent (phylogeny), which provides the basic inherited parameters within which modifications must occur (see Lauder, 1981). Unfortunately, the comparative ontogeny and the higher phylogeny of bats are problems not lavished with attention. The scattered information does, however, permit consideration of several relevant questions.

In most adult microchiropterans, the phaneric, snaillike cochlea simply resembles an earlier embryonic state. The cartilaginous model for the cochlea shows the labyrinthine structure. Moreover, late prenatal stages of growth in members of groups such as the Megachiroptera show a cochlea with incipient petrosal deposition that is indistinguishable from that in adult microchiropterans. What does this pattern imply for cochlear ontogeny in Microchiroptera? One might characterize this ontogeny as some expression of paedomorphosis, that is, the truncation of an ontogenetic component in the descendant taxon with the result that the adult state resembles an earlier (embryonic or ju-

venile) stage of the ancestor. Hence, the theory would suggest that the common bat ancestor had an ontogeny wherein the cochlea was "completely" ossified (i.e., ossified to the extent that its labyrinthine structure was externally cryptic), and one or more times within the microchiropteran lineage this process was interrupted during ontogeny. It should be emphasized that this argument does not specify the nature of the paedomorphic event, namely whether the process involved neoteny (deacceleration), progenesis, or postdisplacement (for formal distinctions, see Alberch et al., 1979: table 1). Ontogenetic data in bats and many other mammals are simply not sufficient for further distinction.

The current literature is replete with arguments on how to interpret the intersection of ontogeny and phylogeny (Fink, 1982; Kluge, 1985; Nelson, 1985; de Queiroz, 1985). This conventional wisdom can be brought to bear on two alternative phylogenies for bat cochlear ontogeny. The truncation event yielding the paedomorphic ontogeny and the phanerocochlear condition in the adult either did or did not occur in the common ancestor of Microchiroptera. A related tissue is the number of times this paedomorphic ontogeny may have arisen. Ontogenies, of course, could be modified or could revert back to their original condition any number of times in a given group. However, the phylogenetic node at which the paedomorphic event first occurred does relate to the total number of ontogenetic changes in the group stemming from this node.

The point can be illustrated by applying a parsimony argument to the simplest possible case of diversity in bat cochlear ontogeny (fig. 5). The outgroups (at least two—see Maddison et al., 1984—although only one outgroup is included in fig. 5) have the complete ontogeny, in which ossification of the cochlea is carried through to a stage where the labyrinthine structure of the cochlea is obscured. The empirical basis for this outgroup condition is fairly secure. Whether or not megachiropterans are the nearest relatives of microchiropterans, in all possible relatives (namely all orders of placental mammals) the adult cryptocochlear condition is probably the ancestral state. Moreover, megachiropterans show no variation in the cryptocochlear condition and, in having this condition, the suborder resembles other mammalian groups. If one regards megachiropterans and microchiropterans as sister groups, it is implausible that the cryptocochlear condition in the former is secondarily derived from the phanerocochlear condition in the bat common ancestor. Thus, the alternatives shown in figure 5C and D are the most likely ones. The ingroup (Microchiroptera) has two different ontogenies, one like the outgroup and one paedomorphic that yields the phanerocochlear adult condition. These alternative ontogenies are expressed universally in each of two monophyletic subgroups. A decision to install the paedomorphic rather than the outgroup ontogeny at the ancestral microchiropteran node increases by one event the number of changes on the tree. Application of parsimony would not favor this decision.

This stripped-down approach to character assessment has its obvious limitations. In cases where the character or ontogeny is unique within the ingroup at some level, parsimony consideration of the constant state in the outgroups will always lead to the same conclusion—namely, the optimized outgroup condition is ancestral for the group in question. This result specifies the condition for the common ancestor of the ingroup and its nearest outgroup. It does not specify the condition of the common ancestor of ingroup taxa. Hence, an application of parsimony based strictly on states distributed among outgroups may ignore highly relevant distributions for the ingroup hierarchy. This is especially important when we consider that many traits that diagnose groups (e.g., ear ossicles of mammals) are highly transformed relative to other groups. In such cases, outgroups may by themselves provide ambiguous information bearing on questions of transformation for the ingroup (Farris, 1982). Hence, a "global" approach to parsimony is advocated, wherein the distributions of states are overlaid on assumed cladistic patterns for both the ingroups and the outgroups (Farris, 1982; Maddison et al., 1984).

Unfortunately, in the case of bats the application of global parsimony collides with a major obstacle. Based on what has been accomplished to date concerning the higher-level relationships of the microchiropteran

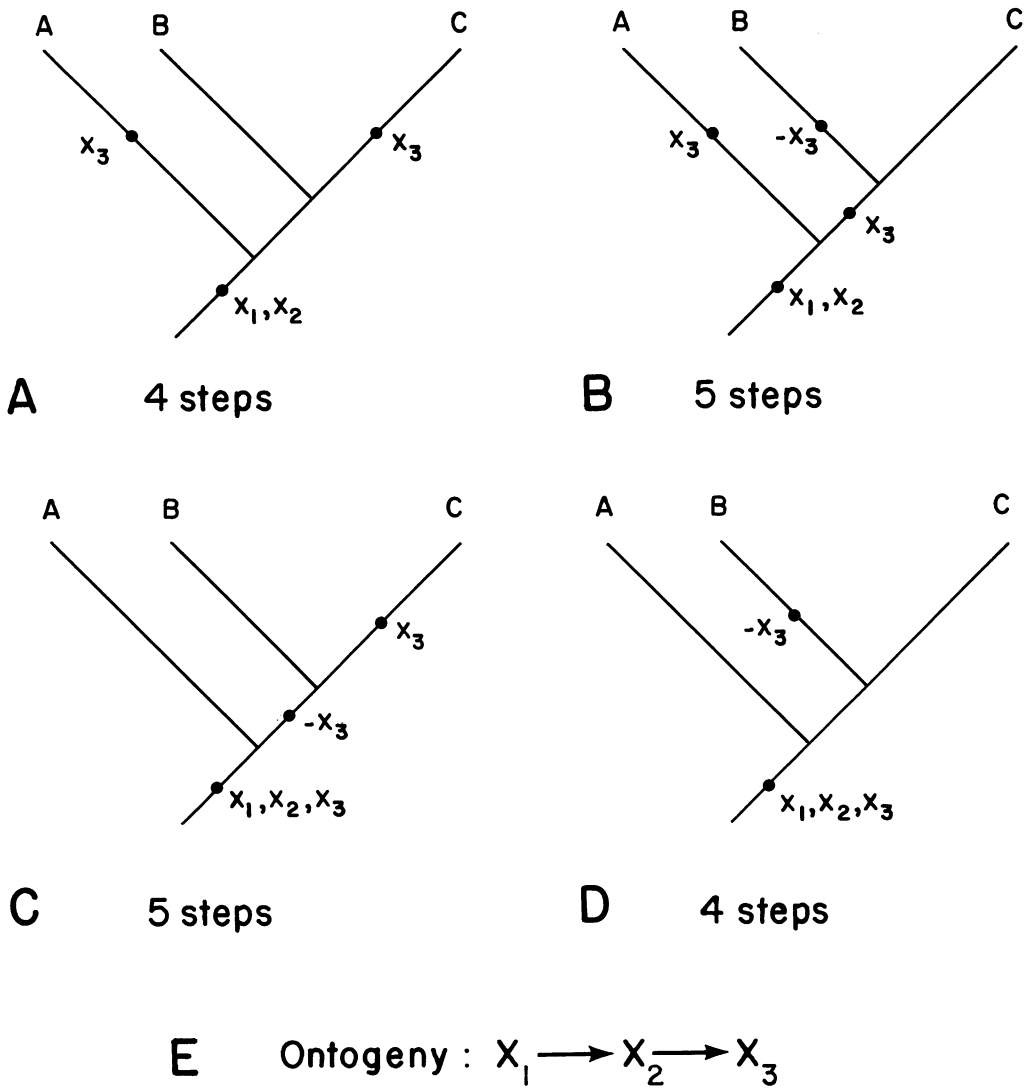

Fig. 5. Parsimony analysis of transformation of cochlear ontogeny. Taxon A is an outgroup with the complete ontogeny (x_1, x_2, x_3). Taxa B and C are lineages of the ingroup (Microchiroptera) that show either the complete ontogeny (x_1, x_2, x_3) (taxon C) yielding the cryptocochlear condition, or the incomplete ontogeny (x_1, x_2) (taxon B) yielding the phanerocochlear condition. The lower diagrams provide for the more reasonable alternative that the complete ontogeny was present in the common ancestor of taxa A, B, and C. The more parsimonious of these (alternative D) calls for the presence of the complete ontogeny at the ancestral node of taxa B and C, with a truncation event ($-x_3$) occurring in the lineage leading to taxon B.

families, it is not safe to assume much, if anything, about a hierarchy for this suborder. Despite a few forays in this area (Hill, 1974; Val Valen, 1979; Novacek, 1980; Smith and Madkour, 1980; Griffiths, 1982; Koopman, 1984; Baker et al., 1989), there are no proposals that account for a reasonable sampling of character diversity in at least all the extant families of bats. Indeed, bats have fared more poorly in this regard than most orders and even a few superordinal groups of mammals (McKenna, 1975; Novacek, 1990).

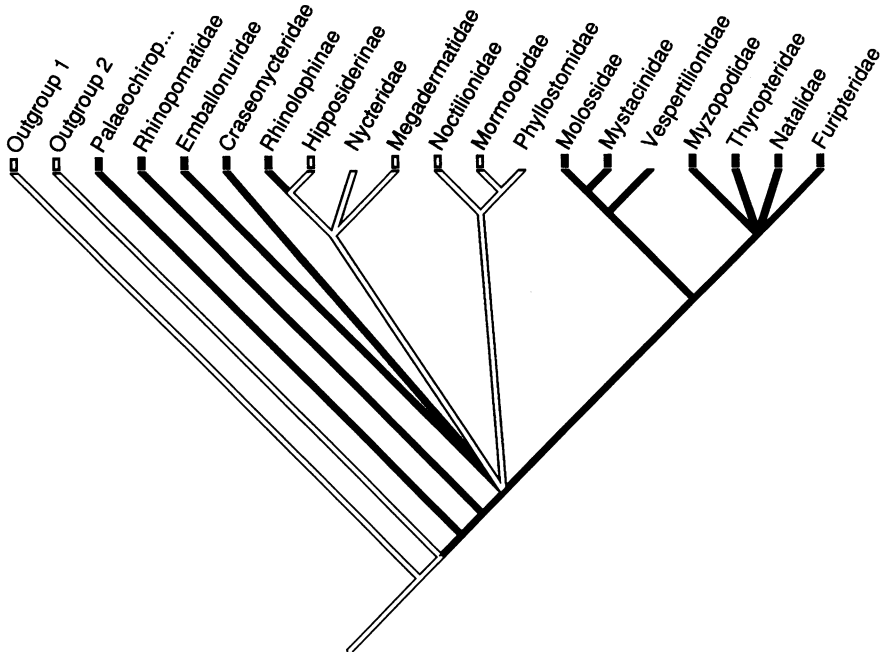

Fig. 6. A global parsimony analysis of cochlear transformation accounting for both ingroup and outgroup distributions of either the cryptocochlear (open boxes) or phanerocochlear (solid boxes) condition. States are not assigned to groups showing significant polymorphism for the cochlear condition. The cladogram reflects characters other than cochlear structure and is based on discussions in Koopman (1984). The position of *Palaeochiropteryx* (Palaeochirop . . .) follows Novacek (1987). Note the remote branch position of Rhinopomatidae. The most parsimonious solution shown here calls for the phanerocochlear condition (solid branches) in the common ancestral node of Microchiroptera. Derivation of the cryptocochlear condition (open branches) occurs at least twice in Microchiroptera. The character transformations require a tree of four steps. Tree produced with MacClade version 2.87e provided by Wayne Maddison.

Despite this obstacle, reference to hypotheses of the higher-level relationships of microchiropterans illustrate the potential impact of ingroup distribution of cochlear ontogenies on decisions concerning the ancestral cochlear ontogeny for the suborder. Equally and even more efficient scenarios are possible if one assumes that the ontogeny yielding the adult phanerocochlear condition is actually ancestral for Microchiroptera (fig. 6). It is noteworthy that several groups showing the phanerocochlear condition are probably early branches of the suborder (e.g., Rhinopomatidae, Emballonuridae, Craseonycteridae, Myzopodidae, and *Palaeochiropteryx*). Moreover, the cryptocochlear condition does not occur in many higher-level taxa. For example, although this trait is consistent for Megadermatidae, this family can be clearly associated with two other groups—the Rhinolophidae and the Nycteridae—within the Rhinolophoidea. The phanerocochlear condition definitely prevails in rhinolophids (fig. 1B), whereas in Nycteridae the occurrence of the cryptocochlear condition varies among species within *Nycteris,* the sole genus in this family. Thus, at least one major group of the Rhinolophoidea shows the phanerocochlear condition shared with other early branches of the Microchiroptera. the same pattern applies for the Vespertilionoidea and the Phyllostomoidea. As a result, even cladograms that reflect a minimum amount of branching among microchiropteran families suggest either than the phanerocochlear condition may be ancestral for the suborder (fig. 6) or that the state is equivocal at this ancestral node (fig. 7).

Fig. 7. A global parsimony analysis as in Figure 5 modified by relocation of the Rhinopomatidae as a sister taxon of Rhinolophoidea (following Pierson, 1985). According to this most parsimonious solution, the ancestral condition for Microchiroptera is equivocal (branches with diagonal hatching). The character transformations require a tree of at least four steps. Tree produced with MacClade version 2.87e provided by Wayne Maddison.

Where does investigation of the problem lead from here? Obviously, as independent morphological and molecular data are gathered, more refined hypotheses of higher-level relationships of bats can be used to assess the distributions of cochlear traits and their ontogenies. A firmer basis for judging the alternatives will thus be available. There are, however, limitations to this procedure. For example, one might not be strictly satisfied with an argument for the ancestral condition that hinges on an optimization one or two steps shorter than an opposing argument.

Another avenue of inquiry is to consider relevant information that bears on our initial concept of the characters and ontogenies in question. Accordingly, we might ask whether the problem of cochlear transformation in bats is simply a question of the phylogenetic level at which paedomorphosis (in the form of arrested ossification of the cochlea) occurs. It is feasible to argue that intertaxon variation in the degree of ossification of the cochlea during ontogeny is simply one of a mosaic of integrated factors. Other components may involve some of the features compared above. For example, it is important that all microchiropterans are characterized by a hypertrophied cochlea, a trait with some, albeit unspecified, relationship to special auditory function. There is also evidence that, overall, this suborder is characterized by a significantly greater coiling of the cochlea than is found in its outgroup relatives. Finally, it should be stressed that although the degree of cochlear isolation varies within Microchiroptera, most taxa show a separation of the cochlea from surrounding basicranial structures that exceeds that observed in outgroup relatives.

If these aspects of the microchiropteran ear are considered as interrelated (Novacek, 1985b), some explanation for their integration is required. Perhaps the arrested ossification of the cochlea may be a way of accommodating the marked expansion of the

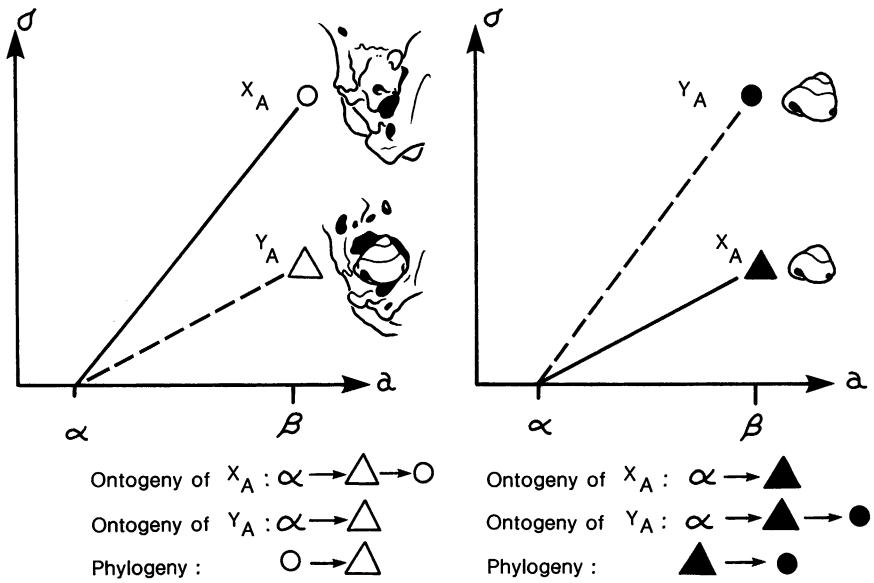

Fig. 8. Scenarios for ontogeny and phylogeny of the bat cochlea following conventions of Alberch et al. (1979). See text for discussion.

cochlea, its increased torsion, and its isolation from other elements of the skull (fig. 8). Relevant here is the observation that in certain bats (*Vespertilio murinus*), apical coiling of the cochlea represents a comparatively late phase in the development of the membranous labyrinth for both the cochlear and vestibular regions (Denis, 1902). Moreover, ossification of the petrosal follows ossification of most other cranial elements in bat species with described ontogenies (Frick, 1954). The pattern is best described as a unique, mosaic ontogeny involving both peramorphosis (enlargement and increased torsion of the cochlea) and paedomorphosis (delay in the onset, truncation, or decreased rate of petrosal ossification).

These basic relationships are depicted in figure 8. The *x*-axis denotes some function of age, the *y*-axis some function of form. Alpha denotes the onset age of growth, beta the offset signal of growth. The argument here is that the phanerocochlear condition in ancestral microchiropterans is a mosaic ontogeny involving at least two components.

The paedomorphic component (fig. 8, left) is represented by the incomplete ontogeny for ossification of the cochlea in the descendant (Y_A). The end point of the ontogeny of the descendant (open triangle) is only an intermediate state in the ontogeny of the ancestor (X_A). The latter ontogeny carries through to a stage symbolized by the open circle. The phylogenetic transformation yields the truncated ontogeny of Y_A.

The peramorphic component (fig. 8, right) is represented by the more complete ontogeny for size increase and torsion of the cochlea in the descendant (Y_A). The end point of the ontogeny of the descendant (closed circle) represents a stage beyond the end point (closed triangle) of the ancestral ontogeny (X_A). The phylogenetic transformation yields the elaborated ontogeny of Y_A.

Note that the ontogenies of the descendant are distinguished by the processes of neoteny (fig. 8, left) and acceleration (fig. 8, right). These are merely used for the purpose of illustration. Other expressions of either paedomorphosis or peramorphosis are possible (see Alberch et al., 1979).

If the scenario depicted in figure 8 applies, the functional significance of the phanerocochlear condition in the adult is at least understandable in ontogenetic terms. Namely, the persistence of this condition is simply a

by-product of the compromise necessary in accommodating the hypermorphosis of the cochlea during late phases of prenatal ontogeny.

The above explanation, however, leaves open the question of origin of the cryptocochlear state in some Microchiroptera. The idea of a highly integrated mosaic ontogeny would predict that ossification would not be arrested in cases where adjustments to the growth of other components were not required. In this regard, it is interesting that nearly all of the cryptocochlear species are relatively large bats. Moreover, a greater or lesser degree of ossification in microchiropterans is often not only characteristic of the petrosal but of the skull as whole. One might speculate that, in smaller echolocating bats, "packing" problems result not only from cochlear expansion but also from the premium on space for ear ossicles, blood vessels, enlarged middle ear muscles (Henson, 1970; Novacek, 1980), nerve tracts, and ganglia. This might account for the relative plasticity among larger species within genera where the cryptocochlear condition occurs.

CONCLUSIONS

Cochlear variation in bats has been associated with particular adaptations for echolocation. Strong comparative and experimental bases for such arguments are, however, not available. Evidence discussed above suggests a strong phylogenetic influence on cochlear variation. There is a case for the supposition that the widespread phanerocochlear condition was ancestral for microchiropterans. The bearing of such a hypothesis on questions concerning the adaptation of bat ear structures awaits a marked refinement of both systematic and functional studies.

Arguments developed in this paper also stress the importance of investigating the interrelationships of components in ontogenies. there are obvious tests concerning the timing of ossification and cochlear expansion that require comparative ontogenetic studies that are not available. At the very least, this example is instructive in revealing the dimensions of problems involving character transformation. Despite the presence of extensively ossified, "cryptic" cochleae in the outgroup relatives of microchiropterans, we are not led to the conclusion that this condition was ancestral for the latter suborder. A variety of factors play a role here, and these point to the clear possibility of a unique and complex ontogeny that is coincident with the origin of this diverse group of mammals. Accordingly, the presence of phaneric or cryptic cochleae in different adult species may be simply an aspect of variation in design that is secondary to the emergence of this unique ontogeny.

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Phylogenetic Relationships of the New World Bat Genus *Sturnira* (Chiroptera: Phyllostomidae)

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ABSTRACT

Phylogenetic relationships of New World leaf-nosed bats of the genus *Sturnira* were analyzed using allozymic and morphological characters. Seven species of *Sturnira* were included in the genetic analyses, and 14 species were included in the morphological survey. Genetic analyses of the monophyly and intergeneric relationships of *Sturnira* utilized a variety of taxa to root trees at different stages of the analysis, including *Sturnira bidens, S. nana, Vampyrops dorsalis, Uroderma bilobatum, Carollia perspicillata, Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis,* all from the family Phyllostomidae. *Sturnira* proved to be more closely related to *Uroderma bilobatum* and *Vampyrops dorsalis* than to *Carollia perspicillata* or *Glossophaga soricina.* These results confirm its current placement with the Stenodermatinae rather than with the Carolliinae or Glossophaginae. The monophyly of *Sturnira* was substantiated, and the subgenus *Corvira* was found to be distinct both genetically and morphologically. Consensus between genetic and morphological analyses further reveals at least two lineages within the subgenus *Sturnira,* the first comprising *S. tildae, S. lilium, S. luisi,* and *S. thomasi,* and the second *S. magna* and *S. erythromos.* Additional materials and analyses will be needed to resolve the positions of other species in the genus.

INTRODUCTION

The genus *Sturnira* is currently placed in the subfamily Stenodermatinae (Chiroptera: Phyllostomidae), which is endemic to the New World tropics. Externally, members of this genus may be recognized by their lack of a tail and the highly reduced interfemoral membrane. *Sturnira* inhabits lowland and humid montane forest from southern Mexico to eastern Brazil, Uruguay, and the West Indies. Eleven or 12 species are currently recognized in two subgenera, *Corvira* and *Sturnira* (Davis, 1980; Honacki et al., 1982).

The species within the genus *Sturnira* appear to be a monophyletic group (Gardner and O'Neill, 1969, 1971; Owen, 1987), but the higher-level relationships of this genus are still enigmatic. Substantial evidence supports its current placement within the Stenodermatinae (de la Torre, 1961; Smith, 1976). (All members of this traditional group were included within the tribe Stenodermatini, subfamily Phyllostominae, in the recently proposed classification of Baker et al. [1989].) Nevertheless, alternative classifications of *Sturnira* have been suggested. For example, Straney et al. (1979) concluded from electrophoretic evidence that *Sturnira* is not a stenodermatine. Following Miller (1907), Walton and Walton (1968) placed the genus in a separate subfamily, Sturnirinae, based on postcranial characters (see also Hall, 1981; Linares, 1986). Slaughter (1970) concluded from tooth structure that *Sturnira* was related to the Glossophaginae. Recently, Phillips et al.

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(1987) found that the parotid secretory granules of *Sturnira* differed widely from those of the other stenodermatines they examined (*Artibeus* and *Ariteus*), being more similar to those of *Trachops* of the Phyllostominae (genus allocated to the Vampyrinae by Baker et al., 1989).

Phylogenetic relationships of *Sturnira* were recently evaluated using discrete-state and mensural characters (Owen, 1987), but many interspecific relationships remained unresolved. Recently, Owen (1988) presented a systematic arrangement of species based on phenetic analyses of mensural data. No other phylogenetic or systematic studies are known to us. Unfortunately, revision of the entire genus *Sturnira* has not been attempted since the study of de la Torre (1961), and several new forms have been subsequently discovered and described.

Without pretending to review all *Sturnira,* this paper investigates phylogenetic relationships of a set of species in the subgenus *Sturnira* using morphological and allozymic sets of data. In addition, we assess the phylogenetic relationships of the genus *Sturnira* within the Phyllostomidae using the allozymic data, and we determine whether the genus *Sturnira* and its subgenera *Corvira* and *Sturnira* are monophyletic. Lack of materials for several taxa makes this analysis incomplete, but it is a first step toward a comprehensive revision of relationships within this diverse and perplexing genus.

Materials and Methods

Cladistic Analysis of Discrete Morphological Characters: A set of cranial, dental, and external characters was analyzed cladistically using the method developed by Hennig (1966). Multiple outgroup taxa were used to polarize the character states, enhancing the prospect of correctly identifying autapomorphic character states in the outgroup. Such uniquely derived characters might otherwise be confused with plesiomorphic character states.

For analyses of interspecific relationships within the subgenus *Sturnira, S. bidens* Thomas, 1915, and *S. nana* Gardner and O'Neill, 1971, of the subgenus *Corvira* were used as outgroups. *Corvira* is considered the sister group for the subgenus *Sturnira* (Gardner and O'Neill, 1969, 1971). Twelve species composed the ingroup: *S. lilium* (E. Geoffroy, 1810); *S. luisi* Davis, 1980; *S. magna* de la Torre, 1966; *S. oporaphilum* (Tschudi, 1844); *S. ludovici* Anthony, 1924; *S. erythromos* (Tschudi, 1844); *S. bogotensis* Shamel, 1927; *S. mordax* (Goodwin, 1938); *S. tildae* de la Torre, 1959; *S. thomasi* de la Torre and Schwartz, 1966; *S. aratathomasi* Peterson and Tamsitt, 1968; and an undescribed species made available to us through the courtesy of Luis Albuja that is here denoted *Sturnira* sp. A. All were examined in the course of this study, and doubtful character states were recorded as missing values.

The analysis was based on a set of 1 external and 14 cranial characters scored mostly from adult specimens (table 1). Characters are described in Appendix 1. The characters were selected after extensive evaluation of characters from a large series of individuals (Appendix 2) and were assumed to be independent. In descriptions of characters, we follow the dental nomenclature of Van Valen (1966) and Phillips (1971).

The character-state matrix was submitted to PAUP (phylogenetic analysis using parsimony) software for personal computers (Swofford, 1985). Parsimony is used to minimize the number of character-state transformations along the branches of a phylogenetic tree. The PAUP options we used were global branch swapping on the first 100 equally parsimonious trees, swapping the remaining trees. This procedure obtains up to 100 equally short trees. The branch-and-bound option, which guarantees obtaining the most parsimonious tree, was not used because of software limitations to nine or fewer taxa. Multistate characters were treated as unordered, freeing the analysis from unwarranted assumptions of particular transitional series. The use of outgroups enabled unequivocal specification of polarity in binary characters.

The CONTREE program with the strict consensus option (SC of Rohlf, 1982) was used to find a single consensus topology among equally short trees identified by the branch swapping analysis. In addition, the jackknife strict consensus method (JSC of Lanyon, 1985) was used on successive iter-

TABLE 1
Character Data Matrix for a Group of Species of the Genus *Sturnira*
(Character and character states are described in Appendix 1)

Species	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sturnira bidens[a]	0	1	0	0	9	0	1	0	0	0	0	0	0	0	0
S. nana[a]	0	1	0	0	9	1	1	0	0	0	0	0	0	0	0
S. sp. A	0	0	0	2	1	1	1	0	0	2	1	1	0	0	0
S. luisi	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0
S. lilium	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0
S. tildae	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1
S. mordax	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0
S. ludovici	1	0	1	1	0	1	0	1	0	1	1	1	0	0	1
S. oporaphilum	1	0	1	1	0	1	0	1	0	1	1	1	1	0	1
S. magna	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0
S. erythromos	1	0	1	1	0	1	0	1	0	1	1	0	2	0	0
S. bogotensis	1	0	1	1	0	1	0	1	0	1	1	0	2	0	0
S. thomasi	1	0	0	1	0	1	0	1	1	1	1	1	1	1	0
S. aratathomasi	0	0	0	2	0	1	0	1	0	1	0	1	0	1	1

[a] Species used as outgroups.

ations of the PAUP and CONTREE algorithms to identify strongly and weakly supported portions of the trees. This method employs successive permutations of the data matrix, deleting a different taxon from the analysis each iteration, to produce a single consensus tree for each of the $n - 1$ data matrices. The resulting strict consensus trees are in turn examined for consensus, producing a final tree that retains the nodes common to the $n - 1$ jackknifed trees.

Owen (1987) presented a topology for the Stenodermatinae, including most of the species of *Sturnira*. His study represents the only published phylogenetic analysis for the genus using discrete morphological data. To homogenize our methodological procedures, we also analyzed his data matrix for species of *Sturnira* using the PAUP algorithm and options outlined above.

ELECTROPHORESIS: Electrophoretic analysis of frozen tissues was done by running aqueous extracts of tissues prepared by standard procedures on horizontal starch gels. The procedures and recipes for buffers and stains followed Selander et al. (1971) and Harris and Hopkinson (1976). Composite samples of liver and kidney were prepared with equal amounts of tissues, homogenized in grinding buffer (pH 7.0), and then centrifuged at 12,000 rpm for 40 minutes. Supernatants were removed and preserved at −70°C until used and the precipitates discarded. Composite homogenates were then used in the subsequent electrophoretic runs.

An initial survey using representative individuals was conducted to determine the most appropriate buffer system for each locus. The optimal buffer systems were then used for the initial analysis of each locus. When the identity of specific electromorphs was uncertain, two to four buffer systems were employed and the taxa in question were compared side by side. Buffer systems, loci examined, and the recent Enzyme Commission numbers of these loci are listed in table 2. Scoring and interpretation of gels were based on Harris and Hopkinson (1976) and Richardson et al. (1986). After runs, the gel itself or the overlaid agar was preserved for future reference. Initially, 29 presumptive loci were surveyed, but 10 were later eliminated from further consideration because of ambiguous or inconsistent scores in repetitive runs or because of uncertain discrimination of electromorphs (ALB, PEP-C, GOT-2, GDH, ODH, EST-D, CK, AK, NP, EAP). The results presented here are based on the remaining 19 presumptive loci: ACON-1, ACON-2, αGPD, GPI, GOT-1, ICD-1, ICD-2, LAP, PEP-B, LDH-1, LDH-2, MDH-1, MDH-2, ME, PEPT-D, PGM, 6-PGD, SOD, and SDH.

Sturnira tissue samples came from 131

TABLE 2
Genetic Loci Analyzed by Electrophoresis, Their Symbols, and the Buffer Systems Used

Symbol	Name	Buffer
ACON-1, 2	Aconitase (E.C. 4.2.1.3)	TC III
GOT-1	Glutamate oxalate transaminase (E.C. 2.6.1.1)	Poulik
αGPD	Glycerophosphate dehydrogenase (E.C. 1.1.1.8)	TC III
GPI	Glucose phosphate isomerase (E.C. 5.3.1.9)	Poulik
ICD-1, 2	Isocitrate dehydrogenase (E.C. 1.1.1.42)	TC II
LAP	Leucine aminopeptidase (E.C. 3.4.11)	TC II
LDH-1, 2	Lactate dehydrogenase (E.C. 1.1.1.27)	LiOH
PEP-B	Peptidase B (E.C. 3.4.11)	Poulik
PEP-D	Peptidase D (E.C. 3.4.11)	Poulik
MDH-1, 2	Malate dehydrogenase (E.C. 1.1.1.37)	TC III
ME	Malic enzyme (E.C. 1.1.1.40)	TM
6-PGD	Phosphogluconate dehydrogenase (E.C. 1.1.1.44)	Poulik
PGM	Phosphoglucomutase (E.C. 2.7.5.1)	Poulik
SDH	Sorbitol dehydrogenase (E.C. 1.1.1.14)	Poulik
SOD	Superoxidase (E.C. 1.15.1.1)	TC II

specimens of the subgenus *Sturnira* and seven of the subgenus *Corvira*. In addition, 25 samples of more distantly related taxa including *Uroderma bilobatum* and *Vampyrops dorsalis* (Stenodermatinae), *Carollia perspicillata* (Carolliinae), *Glossophaga soricina* (Glossophaginae), *Desmodus rotundus* (Desmodontinae), and *Micronycteris megalotis* (Phyllostominae) were used as outgroups at different phases of the analyses. Specimens, localities, and codes for populations are described in Appendix 2.

The first analysis included *Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis* as outgroups to identify the phylogenetic relationships of the genus *Sturnira* with the genera *Uroderma, Vampyrops,* and *Carollia*. The second analysis used *Uroderma* and *Vampyrops* as outgroups to evaluate the monophyly of the subgenera *Corvira* and *Sturnira*. Finally, based on the above analysis and other reported works (Gardner and O'Neill, 1969, 1971; Owen, 1987), *S. bidens* was selected as the outgroup taxon for understanding the systematic relationships among species of the subgenus *Sturnira* that were analyzed: *S. lilium, S. tildae, S. magna, S. luisi, S. erythromos,* and *S. oporaphilum*. Thus, analyses of phylogenetic relationships involving the genus *Sturnira* were pursued from higher to lower taxonomic levels. Allele frequencies for the taxa studied here are summarized in table 3.

Rogers's modified genetic distance (Rogers's *D*; Wright, 1978) and Nei's genetic distance *D* (Nei, 1972), two commonly used measures of genetic distances, were employed. Use of two distance measures can identify the extent to which the structure of dendrograms is independent of the specific assumptions of each measure. Rogers's *D* satisfies the triangle inequality, an important feature for the generation of phyletic trees as discussed by Farris (1981), but it is not proportional to evolutionary time (Nei, 1987). On the other hand, Nei's *D* is roughly proportional to the time of historical divergence, but it may fail to satisfy the triangle inequality due to the logarithmic transformation that is involved (Richardson et al., 1986).

Unrooted Fitch-Margoliash networks (Fitch and Margoliash, 1967) were produced from the matrices of Rogers's *D* and Nei's *D* values using Felsenstein's PHYLIP program (1985). This tree-generating method was selected because it does not assume a constant evolutionary rate among lineages. A jackknife manipulation of taxa was performed with both genetic distances to identify unstable nodes that are presumably poorly supported by the data (Lanyon, 1985). Finally, the root for trees generated by the Fitch-Mar-

goliash method was determined by using one outgroup. Because the main objectives here relate to phylogenetic relationships rather than time of divergence, topologies but not branch lengths are discussed.

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RESULTS

Morphological Analysis

Phylogenetic analyses of the 12 species of the subgenus *Sturnira* were conducted using *S. bidens* and *S. nana* as outgroups (fig. 1). The position of *Sturnira* sp. A is striking, being intermediate between the subgenera *Sturnira* and *Corvira* in several characters. *Sturnira* sp. A shares the presence of the four lower incisors with members of the subgenus *Sturnira.* However, it shares tooth gaps and the absence of zygomatic arch with members of *Corvira.* The position of *Sturnira* sp. A within the cladogram indicates that it could be recognized as a distinct subgenus. Additional specimens are needed to corroborate this assessment or to indicate that it is better considered a primitive member of the subgenus *Sturnira.*

Within the subgenus *Sturnira,* at least two lineages are apparent. The first is composed of *S. ludovici, S. oporaphilum, S. erythromos,* and *S. bogotensis.* These species are closely related in sharing the bilobate condition in the middle lower incisors (character 3). *S. erythromos* and *S. bogotensis* are joined further by the presence of a flat palate (character 13), whereas *S. ludovici* and *S. oporaphilum* share a developed protolophid (character 15); by parsimony, the same state in *S. tildae* (and *S. aratathomasi*) constitutes a parallelism within the subgenus. The second lineage is composed of *S. lilium, S. luisi,* and *S. thomasi.* They share the derived presence of a well-developed entoconid (character 14) and a slightly depressed palate (character 13). Within this lineage, relationships remain unresolved, as do placements of *S. tildae, S. mordax, S. magna,* and *S. aratathomasi.*

Using Owen's character matrix, PAUP resolved the two subgenera of *Sturnira* but left unresolved relationships within the subgenus

TABLE 3
Allele Frequency Data for Phyllostomid Bats

Locus	op-1[a] (1)[b]	op-2 (6)	op-3 (10)	op-4 (5)	bo-1 (7)	er-0 (8)	er-1 (4)	er-2 (1)
ACON-1	b[c]	a(.083) b(.917)	a(.063) b(.937)	b	d	d	d	d
ACON-2	a	a	a	a	a	a	a	a
αGPD	e	e	e	e	d	d(.833) g(.167)	d	d
		N=1	N=1	N=1	N=3	N=6		
GPI	e	e	b(.150) c(.200) e(.650)	b(.100) e(.800) a(.100)	e	e	e	e
GOT-1	b	b	b	b	b	b	b	b
ICD-1	g	g(.666) d(.334)	g(.750) d(.250)	g(.500) d(.500)	d	d	d	d
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b(.700) c(.300)	b	b	b	b
		N=3	N=3		N=6	N=6		
PEP-B[d]	c	c	c	c	c(.714) g(.286)	c	c	c
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a(.900) b(.100)	a	a	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	g	g	g	g	d	d	d	d
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	f	f	f	f	f	f	f	f
6PGD	—	c	c	c	c	b(.125) c(.875)	c	c
SOD	b	b	b	b	e	e	d(.125) e(.875)	e
SDH	e	e	e	e	b	b	b	b

[a] Codes for taxon name and population number are described in Appendix 2.
[b] Sample size for all loci unless mentioned in a specific locus.
[c] Allele frequency equals one unless mentioned in parentheses.
[d] Using leucine-glycine-glycine as substrate.
[e] Using phenylalanine-proline as substrate.

TABLE 3—(*Continued*)

Locus	er-3 (9)	er-4 (1)	er-5 (5)	er-6 (10)	er-7 (2)	er-8 (19)	ma-1 (4)	ma-2 (5)
ACON-1	d(.944) g(.056)	d	d	d	d	d	d(.250) g(.625) i(.125)	d(.100) g(.900)
ACON-2	a	a	a	a	a	a	a	a
αGPD	d	—	d	d(.950) a(.050)	d	d(.816) a(.184)	b	b
	N=4				N=1			
GPI	b(.056) e(.944)	e	e(.900) g(.100)	e	e	c(.026) e(.947) h(.027)	e	e
GOT-1	b	b	b	b	b	b	b	b
ICD-1	b(.056) d(.833) a(.111)	d	d(.900) a(.100)	b(.050) d(.950)	d	a(.026) d(.974)	b	b(.800) d(.200)
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b	b	b	b	b
PEP-B[d]	c	c	b(.100) c(.900)	c	c	b(.026) c(.974)	c	c
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a	a	a(.974) b(.026)	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	d	d	d	d(.950) i(.050)	d	d(.895) i(.105)	d	d
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	c(.056) f(.944)	f	d(.100) f(.900)	d(.050) f(.950)	f	f(.974) i(.026)	c(.875) f(.125)	c(.800) a(.200)
6PGD	c	c	c	b(.100) c(.900)	c	c	c	c
SOD	e	e	e	e	e	e	e	e
SDH	b	b	b	—	—	—	b	b
								N=1

TABLE 3—(*Continued*)

Locus	ti-1 (1)	ti-2 (4)	li-1 (1)	li-2 (1)	li-3 (3)	li-4 (6)	li-5 (7)	li-6 (7)
ACON-1	d	b(.125) d(.875)	c(.500) f(.500)	h	c(.667) f(.167) h(.166)	c(.917) f(.083)	c(.500) f(.500)	c(.786) f(.071) e(.143)
ACON-2	a	a	a	a	a	a(.750) b(.250)	a	a
αGPD	d	d	d	d	d	d	d N=6	d N=3
GPI	e	e	e	e	e	e	e	e
GOT-1	b	b	b	b	b	b	b	b(.929) c(.071)
ICD-1	d	g(.375) d(.625)	g(.500) i(.500)	g	g(.667) i(.333)	g(.667) i(.333)	g(.571) i(.429)	g(.929) c(.071)
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b	b	b	b	b
PEP-B[d]	c	c	c	c	c(.500) e(.333) g(.167)	c(.917) e(.083)	c	c(.929) f(.071)
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a	a	a	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	g	g	g	g	g	g	g	g
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	f	f	h	f(.500) i(.500)	f(.500) h(.333) i(.167)	f(.250) h(.667) i(.083)	f(.143) h(.786) i(.071)	f(.429) h(.571)
6PGD	c	c	c	c	c	c	c	c
SOD	b	b	d	d	d	b(.167) d(.833)	b(.286) d(.714)	d
SDH	—	g N=2	—	e	e	e(.833) f(.167)	e	—

TABLE 3—(*Continued*)

Locus	lu-1 (2)	bi-1 (7)	vd-1 (5)	ub-1 (7)	cp-1 (10)	dr-1 (1)	gs-1 (1)	mm-1 (1)
ACON-1	c	l	c	j	l	k	—	l
ACON-2	a	a	b	b	b	—	—	—
αGPD	d	a	d	c	d	g	e	f
GPI	e	g	f	f	N=7 g	c	i	a(.500) d(.500)
GOT-1	b	b	b	d	a	e	c	f
ICD-1	d	e	f	c(.214) e(.786)	h	i	e	g
ICD-2	d	c	a	a	a	a	a	b
LAP	b	b	b(.700) a(.300)	b	b	—	—	—
PEP-B[d]	c	b(.357) c(.571) e(.072)	c	e(.071) g(.786) h(.143)	b	d	a	i
LDH-1	a	a	a	a	b	c	c	c
LDH-2	a	a	a	a	b	c	e	d
MDH-1	a	a	a	a	a	a	a	a
MDH-2	b	b(.714) c(.143) a(.143)	b	b	b	b	b	b
ME	i	e	h	f	c	b	j	a
PEP-D[e]	c	c	d	d	b	d	d	a
PGM	f(.750) b(.250)	f	h	g(.071) h(.929)	f	d	b(.500) e(.500)	c
6PGD	c	c	c(.667) f(.333) N=3	c(.929) e(.071)	c	c	d	a
SOD	b	c	a	d	f	f	g	e
SDH	—	b	b	b	a	d	—	c

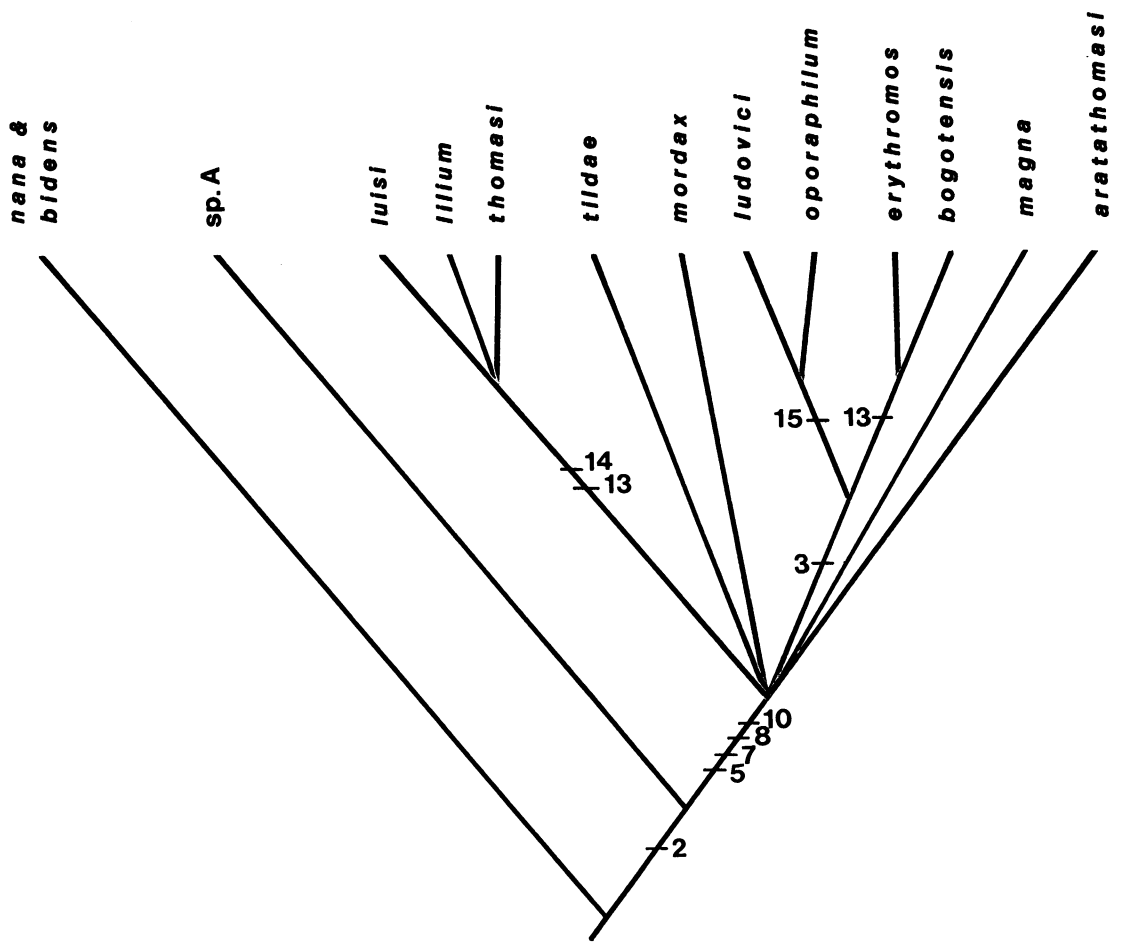

Fig. 1. Final strict consensus cladogram of species of the subgenus *Sturnira,* based on discrete morphological characters (table 1). *Sturnira bidens* and *S. nana* were used as outgroups. Numbers refer to derived morphological characters described in Appendix 1.

Sturnira (see also Owen, 1987, and his fig. 17). Because Owen's characters were selected for assessing higher-level relationships within the Stenodermatinae, they are not as useful for discerning interspecific relationships within speciose genera like *Sturnira.* Apparently, different sets of characters are needed to resolve relationships at different taxonomic levels.

Electrophoretic Analyses

Interspecific Variability: Loci with allelic frequencies higher than 0.95 were considered monomorphic (LDH-1, LDH-2, PEPT D). The average polymorphism value for *Sturnira* species was $P = 0.134$, with a range from 0.053 to 0.237 (table 4). These values are comparable to the value $P = 0.147$ given for mammals (Nevo, 1978) and are similar to an average of $P = 0.164$ that we have obtained from data for 25 phyllostomid bats (Koop and Baker, 1983) or $P = 0.141$ from a broader group of Neotropical bats (Straney et al., 1979). Heterozygosity values, H, ranged from 0.0197 in *S. luisi* to 0.0963 in *S. lilium.* These H values are also comparable to $H = 0.036$ given for mammals (Nevo, 1978), to $H = 0.037$ obtained from data for phyllostomid bats (Koop and Baker, 1983), and $H = 0.032$ from data in Straney et al. (1979).

Matrices of genetic distance values (Nei's *D* and Rogers's *D*) for all the Phyllostomidae analyzed here were based on 15 loci (table 5). Four loci (ACON-1, ACON-2, LAP, SDH) were not included because they were not shared by all the taxa. The same distance values for the stenodermatine species were based on 19 loci (table 6), accounting for minor differences between pairwise distance estimates in the two tables. The range of Nei's *D* among species of the subgenus *Sturnira* was 0.329–0.541 (Rogers's *D*, 0.121–0.358), whereas the distance between species of the subgenus *Sturnira* and the subgenus *Corvira* was higher, 0.615–0.656 (Rogers's *D*, 0.513–0.603). These values are grossly comparable to those of other mammalian taxa (Avise and Aquadro, 1982).

GENETIC DISTANCE ANALYSES: Relationships of taxa were inferred from genetic distance matrices of Nei's *D* and Rogers's *D* using the Fitch-Margoliash algorithm. Analysis of *Sturnira* was initially conducted using non-stenodermatine taxa (*Micronycteris megalotis, Desmodus rotundus, Glossophaga soricina*) to root the trees (fig. 2) and later using the stenodermatines *Vampyrops dorsalis* and *Uroderma bilobatum* for this purpose (fig. 3). Trees generated with Nei's *D* and Rogers's *D* differed in branch length but had identical topologies; only trees using Nei's *D* are shown.

The depicted pattern of relationships among the genera showed a closer relationship of *Sturnira* to other stenodermatines (*Uroderma, Vampyrops*) than to *Carollia* or *Glossophaga,* supporting the inclusion of *Sturnira* within the Stenodermatinae. In addition, these dendrograms showed the genus *Sturnira* as a natural group and consistently placed *S. bidens* at the base of the remaining *Sturnira* species. These analyses support the use of *S.* (*Corvira*) *bidens* as an outgroup for investigating relationships among species of the subgenus *Sturnira.*

Relationships within the subgenus *Sturnira* were evaluated using *S. bidens* to root the trees (fig. 4). The average percent standard deviation for 45 trees was 5.09 for Nei's *D* and 8.65 for Rogers's *D.* Because we are inferring phylogenetic relationships from topologies, branch distances were not analyzed. Two lineages were identified in figure 4: *S. oporaphilum* clusters with *S. tildae,* followed by *S. lilium* and *S. luisi,* whereas *S. erythromos* and *S. magna* compose a second group.

TABLE 4

Proportion of Polymorphic Loci and Heterozygosity Based on 19 Loci for the Species Here Examined

Species	N	Polymorphism, *P* (%)	Heterozygosity, *H*
Sturnira bidens	7	10.5	0.0521
S. oporaphilum	16	15.8	0.0530
S. erythromos	55	17.6	0.0304
S. magna	9	13.2	0.0413
S. tildae	4	15.8	0.0362
S. lilium	23	23.7	0.0963
S. luisi	2	5.3	0.0917
Vampyrops dorsalis	5	10.5	0.0455
Uroderma bilobatum	7	21.1	0.0503
Carollia perspicillata	10	0	0

Finally, pseudoreplicates were calculated to assess the robustness of these associations (Lanyon, 1985). As before, topologies of trees based on the two genetic distances were identical. The grouping of *S. tildae* and *S. oporaphilum* was not retained, and *S. tildae, S. oporaphilum, S. luisi,* and *S. lilium* composed an unresolved group. However, the node comprising *S. erythromos* and *S. magna* was retained in pseudoreplicates and appears to signify the special affinities of these taxa (fig. 5).

DISCUSSION

The position of *Sturnira* with respect to other phyllostomids and interspecific and subgeneric relationships within the genus are illuminated by cladistic analyses of morphology and genetics. Rather than cede superiority to one of these data sets, we have emphasized congruence in our analyses. Congruence among character sets is likely to reveal underlying historical patterns of relationship (Hillis, 1987).

Various workers (de la Torre, 1961; Baker, 1973; Smith, 1976; Gardner, 1977; Owen, 1987) have concluded that *Sturnira* is a member of the Stenodermatinae, while others have placed the genus outside the sub-

TABLE 5

Matrix of Genetic Distances for Phyllostomid Species Generated from Allele Frequency Data (table 3)

(Above the diagonal are modified Rogers's *D*, below Nei's *D*)

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *Sturnira oporaphilum*	—	0.1839	0.2659	0.1954	0.3743	0.0852	0.5337	1.2990	1.0562	1.5586	1.5717	1.6804	0.7709
2. *S. lilium*	0.3948	—	0.2433	0.2294	0.3515	0.1190	0.6095	1.2016	0.7695	1.4785	1.9402	1.6426	0.5451
3. *S. erythromos*	0.4712	0.4491	—	0.1474	0.1836	0.1524	0.5390	1.1066	1.0605	1.5889	1.9835	1.5755	0.6573
4. *S. luisi*	0.4129	0.4399	0.3639	—	0.3611	0.0822	0.5774	1.1372	1.0673	1.5968	1.9247	1.9853	0.6435
5. *S. magna*	0.5464	0.5276	0.4017	0.5426	—	0.3615	0.6639	1.5745	1.0634	1.5929	1.9814	1.3308	0.7794
6. *S. tildae*	0.2800	0.3255	0.3693	0.2772	0.5424	—	0.5452	1.0844	1.0658	1.5952	1.9838	1.8440	0.6419
7. *S. bidens*	0.6233	0.6485	0.6277	0.6471	0.6792	0.6330	—	1.0503	0.9483	1.6754	1.6584	2.1180	0.8751
8. *Carollia perspicillata*	0.8410	0.8171	0.8093	0.8190	0.8832	0.8079	0.7930	—	1.3067	1.0986	1.5925	1.9980	1.1526
9. *Uroderma bilobatum*	0.7832	0.7037	0.7866	0.7918	0.7894	0.7909	0.7568	0.8403	—	1.0800	1.0924	1.9649	0.5143
10. *Desmodus rotundus*[a]	0.8763	0.8585	0.8825	0.8874	0.8853	0.8866	0.8866	0.8165	0.7997	—	1.0817	1.5925	1.1526
11. *Glossophaga soricina*[a]	0.8702	0.8961	0.9108	0.9106	0.9131	0.9143	0.8771	0.8851	0.7952	0.8062	—	1.5755	1.2898
12. *Micronycteris megalotis*[a]	0.8819	0.8697	0.8734	0.9152	0.8435	0.9033	0.9144	0.9220	0.9044	0.8851	0.8756	—	1.9829
13. *Vampyrops dorsalis*	0.7174	0.6286	0.6814	0.6794	0.7242	0.6783	0.7452	0.8210	0.6192	0.8210	0.8378	0.9139	—

[a] Species used as outgroups.

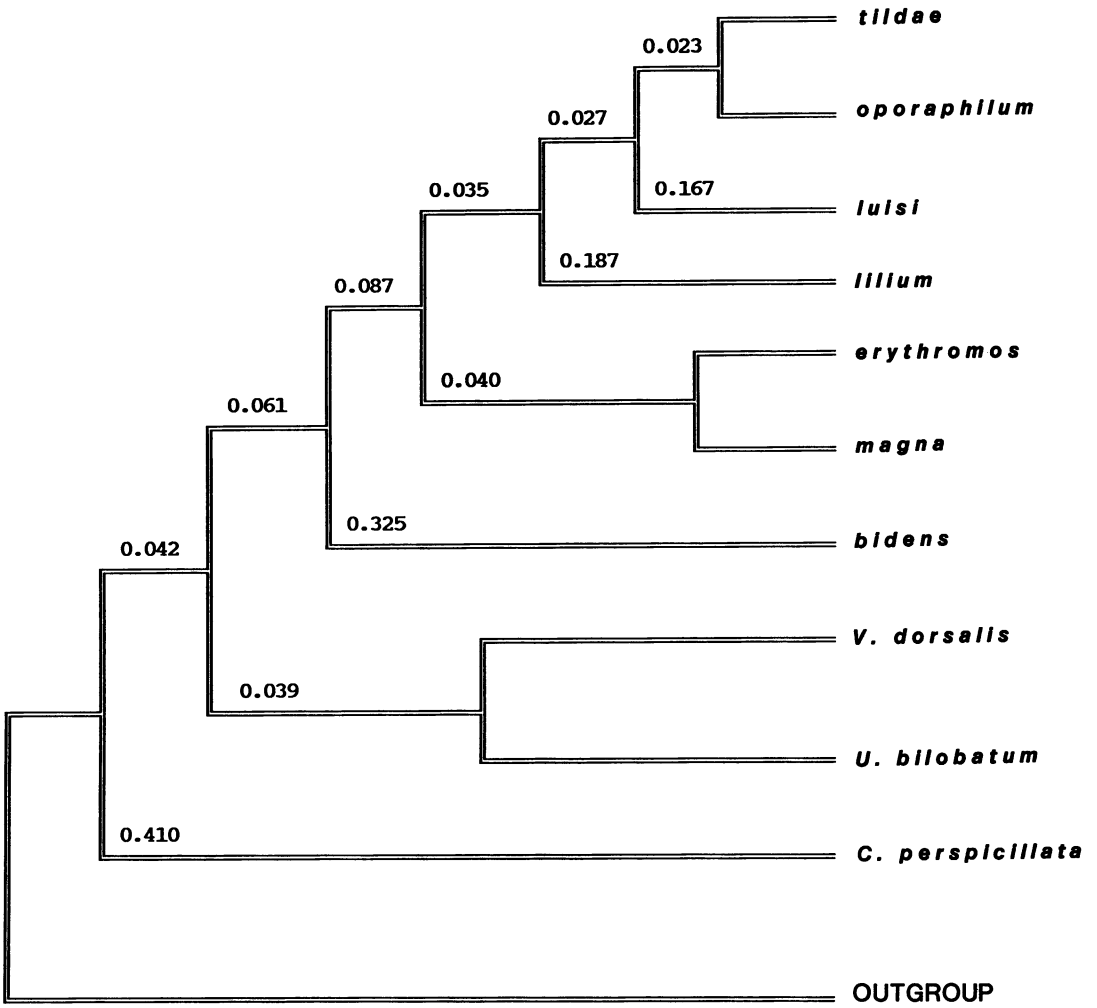

Fig. 2. Fitch-Margoliash dendrogram based on Nei's genetic distances, depicting phylogenetic relationships of four genera of Phyllostomidae. *Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis* were used as outgroups. Dendrogram was derived from table 5.

TABLE 6

Matrix of Genetic Distances Generated from Allele Frequency Data (Table 3)

(Above the diagonal are modified Rogers's *D*, below Nei's *D*)

	1	2	3	4	5	6	7	8	9
1. *Sturnira oporaphilum*	—	0.2061	0.2888	0.2285	0.3705	0.1213	0.5130	1.0757	0.8511
2. *S. lilium*	0.4128	—	0.2561	0.1941	0.3371	0.1445	0.5580	0.7945	0.5455
3. *S. erythromos*	0.4882	0.4582	—	0.1867	0.1953	0.1259	0.5140	1.0666	0.7440
4. *S. luisi*	0.4426	0.4072	0.4068	—	0.3580	0.1253	0.5454	1.0727	0.6181
5. *S. magna*	0.5408	0.5139	0.4123	0.5392	—	0.3409	0.6034	1.0590	0.8446
6. *S. tildae*	0.3299	0.3544	0.3379	0.3385	0.5266	—	0.5144	1.0663	0.7246
7. *S. bidens*	0.6145	0.6267	0.6193	0.6360	0.6557	0.6200	—	0.9732	0.9425
8. *Uroderma bilobatum*[a]	0.7877	0.7098	0.7914	0.7960	0.7876	0.7920	0.7671	—	0.5113
9. *Vampyrops dorsalis*[a]	0.7356	0.6226	0.7089	0.6672	0.7369	0.7032	0.7609	0.6165	—

[a] Species used as outgroups.

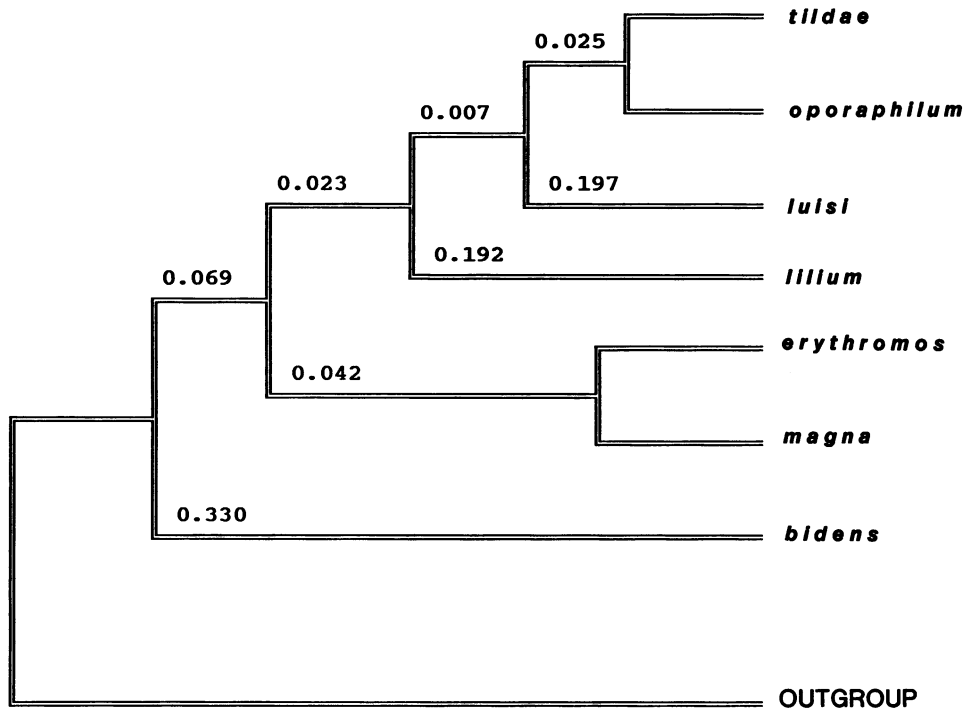

Fig. 3. Fitch-Margoliash dendrogram of the genus *Sturnira* based on Nei's genetic distances in table 6. *Uroderma* and *Vampyrops* were used as outgroups.

family (Walton and Walton, 1968; Slaughter, 1970). Herein, the placement of *Sturnira* within the Stenodermatinae is supported by allozymic data. Figure 2 shows that *Sturnira* is more closely related to the stenodermatines *Vampyrops* and *Uroderma* than to *Carollia* or *Glossophaga*. The latter two genera have traditionally been placed in separate subfamilies (Carolliinae and Glossophaginae, respectively), but Baker et al. (1989) included both in their Phyllostominae, *Carollia* as a member of the Stenodermatini and *Glossophaga* in the Glossophagini. Results in figure 2 indicate that, if *Carollia* is a member of a broadened stenodermatine clade, it is a basal member less closely related to typical stenodermatines than is *Sturnira*. Our alignment of *Sturnira* with *Vampyrops* and *Uroderma* contradicts earlier allozymic evidence that *Sturnira* is not a stenodermatine (Straney et al., 1979), but that study may be unreliable concerning relationships of *Sturnira* (Straney, personal commun.).

Owen (1987) demonstrated the monophyly of the genus *Sturnira* in his phylogenetic analyses of Stenodermatinae using discrete and continuous morphological characters. Here, the monophyly of *Sturnira* is supported by allozymic data. Although few other species of Phyllostomidae were analyzed in this study, their representation among subfamilies or tribes permits reliable tests of the monophyly of *Sturnira*. All seven species of the genus *Sturnira* cluster together in analyses using both the stenodermatines *Uroderma* and *Vampyrops* (fig. 3) and nonstenodermatine taxa to root the trees (fig. 2). Monophyly of the genus justifies our subsequent analyses of intrageneric relationships.

Within the genus *Sturnira*, *S.* (*Corvira*) *bidens* differed genetically from all species of the subgenus *Sturnira*. Nei's *D* and Rogers's *D* between *S. bidens* and other *Sturnira* were always greater than between any pair of species of the subgenus *Sturnira* (table 6). These results support the recognition of the subgenera *Corvira* and *Sturnira*.

Several discrete morphological character

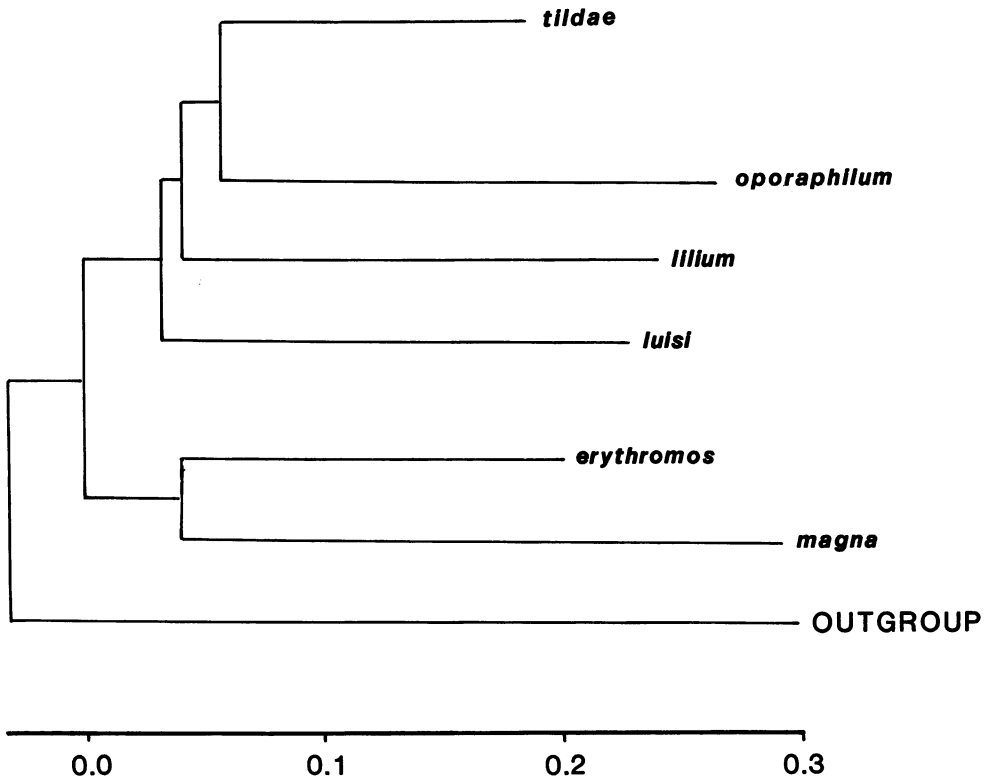

Fig. 4. Fitch-Margoliash dendrogram of the subgenus *Sturnira* based on Nei's genetic distances in table 6. *S.* (*Corvira*) *bidens* was used as the outgroup.

states differentiate the species of the subgenus *Sturnira* from the two species of the subgenus *Corvira* (fig. 1). Using different discrete characters, Owen (1987) arrived at the same conclusion, but the distinctiveness of *Corvira* was not apparent in phenetic analyses of continuous characters (Owen, 1987, 1988). He retained the subgeneric status of *Corvira,* following Gardner and O'Neill (1969, 1971). Genetic and morphological results here suggest that the subgenus *Corvira* is well defined and highly differentiated from other *Sturnira.* Based on our morphological analyses, *Sturnira* sp. A also appears to be a distinct but unnamed subgenus that is somewhat more closely related to the subgenus *Sturnira.* Additional specimens of this species are needed to substantiate this conclusion.

Some of the morphological characters used in our analysis were previously reported (de la Torre, 1961; Davis, 1980) but had been used mostly in the context of identification keys rather than in a formal phylogenetic analysis. For example, de la Torre (1961) used the lingual notch in the lower molar series to divide all *Sturnira* into "serrated" or "not serrated" species, treating *Sturnira bidens* as another "not serrated" species. On the other hand, Davis (1980) employed the same character only after removing *S. bidens* and *S. nana* (the subgenus *Corvira*) by their possession of two lower incisors. Here, 15 selected characters were used for the first time in an unweighted parsimony approach to construct a phylogeny. After comparing the resulting cladogram with a corresponding genetic dendrogram, we generated a hypothesis of phylogenetic relationships within the genus.

In the morphological cladogram, *Sturnira lilium, S. luisi* and *S. thomasi* compose a single lineage. *S. thomasi* was not included in the genetic analysis, which separated *S. lilium, S. luisi, S. tildae,* and *S. oporaphilum* as a distinct lineage. The close relationship

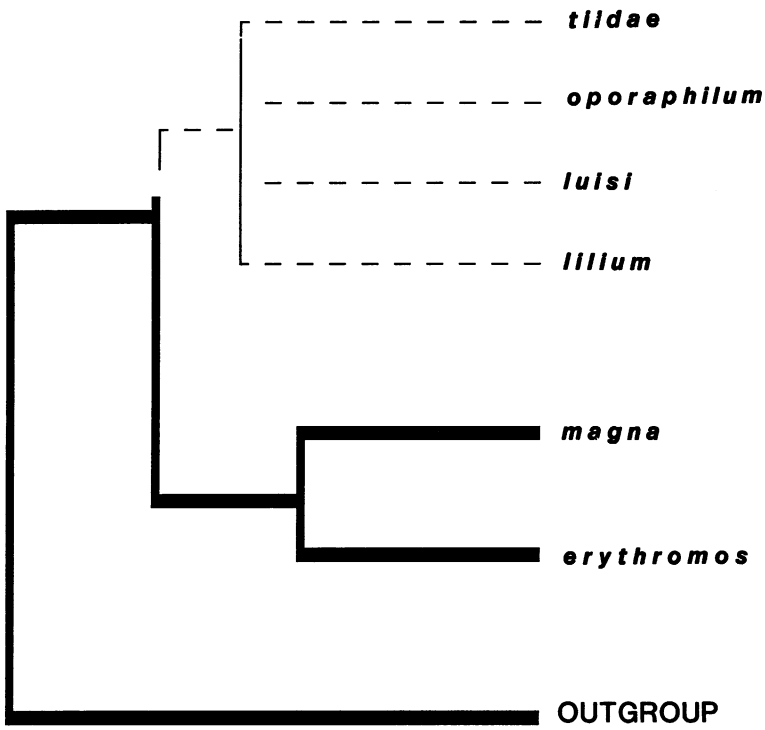

Fig. 5. Jackknife strict consensus tree based on figure 4 for species of the subgenus *Sturnira*. Bold lines indicate nodes that were stable to all permutations of the data matrix; dashed lines indicate unstable relationships.

of *S. lilium* and *S. luisi* is thus supported by both morphological and genetic data, although jackknife analyses of the genetic data call this association into doubt.

The jackknife strict-consensus tree based on allozymes strongly supported the node linking *Sturnira magna* and *S. erythromos*. However, in the cladogram based on morphology, the position of *S. magna* could not be resolved, and *S. erythromos* was joined to *S. ludovici, S. oporaphilum,* and *S. bogotensis*. Additional evidence supports the phylogenetic relationship of *S. magna* and *S. erythromos*. Both species possess an acrocentric Y chromosome, whereas *S. lilium* and *S. ludovici* have a subtelocentric Y chromosome (Gardner, 1977; Baker et al., 1982). Furthermore, the first lower molars of *S. magna* and *S. erythromos* are quite similar, with a small metaconid present and the protolophid and entoconid both absent.

In the cladistic analyses of morphology, *Sturnira bogotensis* was allied with *S. erythromos* rather than *S. oporaphilum,* despite the similar size of *S. bogotensis* and *S. oporaphilum*. *S. bogotensis* can be easily differentiated from *S. oporaphilum* and *S. ludovici* by the absence of the protolophid in the first lower molar (character 15). Detailed studies of the status of these taxa and their geographic variation will be reported elsewhere (Pacheco, in prep.).

The genetic dendrograms suggest that *Sturnira tildae* is related to *S. lilium* and *S. luisi,* but its position in the morphological cladogram is unresolved. Similarly, consensus is lacking for the placement of *S. oporaphilum*: morphology places it in a lineage with *S. ludovici, S. erythromos,* and *S. bogotensis,* while genetic data place it with *S. tildae, S. lilium,* and *S. luisi.*

We cannot choose on logical grounds between statements of relationship based on morphological characters and those summarized in the genetic dendrograms. A hypothesis of phylogenetic relationships within

Sturnira based on congruence of these analyses identifies two lineages: *Sturnira tildae, S. lilium, S. luisi,* and *S. thomasi* form one lineage, and *S. erythromos* and *S. magna* compose the second. Positions of other species in the subgenus *Sturnira* relative to these groups cannot be resolved. However, based on morphological similarities, *S. ludovici–S. oporaphilum* and *S. bogotensis–S. erythromos* seem to be sister pairs. Obviously, additional studies including the species not analyzed here are needed.

Morphologically, *Corvira* is distinguished mainly by the loss of characters distinguishing other taxa of *Sturnira,* rather than by the acquisition of novel apomorphic character states. Examples include the reduction or lack of zygomatic arch, the gaps among the cheek teeth, the reduced molar cusps, and the tendency for reduced number of lower incisors (Miller, 1907; Gardner and O'Neill, 1969, 1971). Instances of evolutionary loss complicate the identification of character states in common ancestors, whose existence can be inferred from monophyly. Based on the morphology of typical stenodermatines and of mammals generally, it seems probable that species of the subgenus *Corvira* were derived from an ancestor that resembled members of the subgenus *Sturnira.* In turn, this implies that the species of *Corvira* have undergone faster evolutionary differentiation (i.e., more rapid acquisition of apomorphic states in the characters under study) than members of the subgenus *Sturnira.*

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APPENDIX 1: DESCRIPTION OF MORPHOLOGICAL CHARACTERS

1. Shoulder glands: Externally indicated by a tuft of stiff modified hairs at front of shoulders, occurring mostly in adult males (Miller, 1907). 0, absent; 1, present.

2. Number of lower incisors: The outer lower incisors may sometimes be present as simple spicules (Gardner and O'Neill, 1971), in which case only the inner incisors were counted. This suggests that four teeth represents the primitive condition. 0, four present; 1, two present.

3. Number of lobes of inner lower incisors (i1): Scores from juveniles and subadults were used when the adult scores were misleading because of tooth wear. The outer lower incisors were not scored because they were apparently more prone to wear than the inner ones. 0, three lobes present; 1, two lobes present.

4. Inner lower incisors (i1) with median lingual cusp: This structure appears to be a modification of the posterior border of the cingulum; in old specimens it is affected by wear. 0, present; 1, small; 2, absent.

5. Shape of lower incisors: Defined by the shape of outline. Curved shape means a slight convexity outlined by the anterior border of the teeth; triangular shape is caused by highly protruded incisors. When only two incisors were present, we scored it as a missing value because the shape produced by two teeth did not logically apply (Swofford, 1985). 0, curved; 1, triangular.

6. Cingulum of the lower canines: Two canine types are apparent among the species of *Sturnira*: slender and broad. The latter is apparently the result of greater development of the cingulum. 0, slender; 1, broad.

7. Tooth gaps: These are spaces between premolars and molars apparently produced by the reduction of the paracone(id). We scored *Sturnira mordax* as not having gaps, although the scored specimen presented an incipient or vestigial gap among the molars, but the paracone(ids) were not reduced. Other *Sturnira* species rarely presented indications of gaps, especially between molars, either in the upper or the lower jaw. 0, gaps absent; 1, gaps present.

8. Zygomatic arch: An incomplete zygomatic arch among the *Sturnira* was considered homologous based on the underlying similarities of the squamosal bone. The absence of zygomatic arches in the presumably related genera such as *Carollia* seems not homologous to that character in *Sturnira*. The two taxa differ in the orientation of the squamosal, being mainly horizontal in *Sturnira* and vertical in *Carollia*. 0, absent; 1, present.

9. Posterior third lower molar (m3): Although the absence of the third lower molar can be correlated with other tendencies for reduction, such as dental gaps, it is considered uncorrelated with other characters. Some individual variation was noted. 0, present; 1, absent.

10. Posterior internal basal cusp in inner upper incisor (I1): This character could be homologous with the lingual cusp of the lower incisors (character 4). However, because of the distinct shape of these structures they were considered independent. 0, present; 1, intermediate; 2, absent.

11. Lobes of inner upper incisors (I1): This character was difficult to score in some taxa because it is quickly worn. Linares (1986) indicated that *bogotensis* differs from *erythromos* in tending to have entire incisors, not the distinct bilobate incisors of *erythromos*. We have observed the bilobate state in juveniles and subadults of *bogotensis* and entire incisors in adults of *erythromos*. Whenever available, juveniles or subadults were scored. Number of lobes (one or two) was scored without consideration of their size. 0, one lobe; 1, two lobes.

12. Orientation of upper inner incisors (I1): The direction of the incisors was considered relative to the course of the upper canines. Incisors following the curve of the upper canines were called curved and those oriented more forward or separate from the upper canines were termed protruded. This character was also difficult to score because it is affected by sexual dimorphism. The males of some species have more protruded incisors than do females (e.g., *Sturnira magna*). 0, curved; 1, protruded.

13. Palate depth: Adults have either a "depressed" or a "flat" palate. Depressed indicates a concavity in transverse view, usually with a conspicuous but narrow longitudinal groove; a flat palate is more planar or slightly concave but without a narrow groove. An intermediate score was included because it proved to be constant in the observed series. This character is strongly affected by age, with juveniles and subadults having a more depressed and narrow palate than adults. This developmental variation can confuse identification, in which case states may be recognized by the width of the palate. 0, depressed palate; 1, slightly depressed with rare presence of narrow groove; 2, flat palate.

14. Entoconid of first lower molar (m1): We have chosen this character because it seems to represent a complex molar pattern in a simple way. It partially corresponds to the "serrated or not serrated" lower molars of Davis (1980) and to the "vertical division" between the metaconid and en-

toconid of de la Torre (1961). 0, absent; 1, developed.

15. Protolophid in first lower molar (m1): Ridge between the protoconid and the metaconid of the first lower molar. It is also associated with the distance between the two cusps. The protoconid and metaconid are much closer together when the protolophid is present than when it is not. When the protolophid was not clearly observable, the distance between the cones indicated the pattern. The character was observed in all age classes and was still visible (when present) in worn teeth. 0, absent; 1, developed.

APPENDIX 2: SPECIMENS EXAMINED IN THE CLADISTIC AND ELECTROPHORETIC ANALYSES

Codes used in table 3 are in boldface type in parentheses. * Specimens used only in the cladistic analysis. † Specimens used only in the electrophoretic analysis. Museum acronyms are as follows: AMNH, American Museum of Natural History; EPN, Escuela Politécnica Nacional, Ecuador; FMNH, Field Museum of Natural History; LSUMZ, Museum of Zoology, Louisiana State University; MSB, Museum of Southwestern Biology, University of New Mexico; MVZ, Museum of Vertebrate Zoology, University of California; MZUSP, Museu de Zoologia, Universidade de São Paulo, Brazil; TTU, The Museum, Texas Tech University; USNM, National Museum of Natural History (United States).

Carollia perspicillata†: PERU: Amazonas, 3 km E Balzas, FMNH 128764–128768; Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128773–128777 (**cp-1**).

Desmodus rotundus†: PERU: Lima, San Bartolomé, Rímac Valley, FMNH 129204 (**dr-1**).

Glossophaga soricina†: PERU: Amazonas, 3 km E Balzas, FMNH 128681 (**gs-1**).

Micronycteris megalotis†: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2103 (MZUSP uncatalogued) (**mm-1**).

*Sturnira aratathomasi**; COLOMBIA: Valle del Cauca, Pance, ca. 20 km SW Cali, USNM 395158.

Sturnira bidens: PERU: Piura, "Batan" on Zapalache–Carmen trail, LSUMZ 26920–26922; "Machete" on Zapalache–Carmen trail, LSUMZ 26915–26916; "Lucuma" on Zapalache–Carmen trail, LSUMZ 26919; Cerro Chinguela, ca. 5 km NE Zapalache, LSUMZ 26924 (**bi-1**).

*Sturnira bogotensis**: COLOMBIA: Bogotá, La Uribe, USNM 251986–251987. Santander, Puente Nacional, AMNH 207851. Bogotá, Base de Monserrate, AMNH 207852–207857. Cundinamarca, Bogotá, AMNH 207858–207860; Mesitas del Colegio, AMNH 207861–207862; Sibate, AMNH 212276; Usaguen, N of Bogota, AMNH 62798; Choachi, Bogotá region, AMNH 61556; Bogotá, USNM 251988. Bogotá, Estacion La Uribe, USNM 251989. VENEZUELA: Merida, Montes de Lourdes, AMNH 24378; Tachira, 35 km S, 22 km W of San Cristobal (Buena Vista), USNM 440088.

Sturnira erythromos: PERU: Lima, San Bartolomé, FMNH 128789–128792; Bosque de Zarate, FMNH 128935, 128793–128794 (**bo-1**). Ancash, Río Mosna, FMNH 128781–128788 (**er-0**). Amazonas, 19 km (by road) E Balzas, FMNH 128796–128799 (**er-1**); Río Utcubamba, between Churuja and Pedro Ruiz, FMNH 128809 (**er-2**); ca. 20 km (by road) W Leymebamba, FMNH 128800–128808 (**er-3**). Cajamarca, Río Zaña, 2 km N Monteseco, FMNH 128811 (**er-4**). Cuzco, 32 km NE Paucartambo (km 112), MVZ 171436–171437, 171440–171442 (**er-5**). Piura, Cruz Blanca, 33 km road SW Huancabamba, LSUMZ 26930–26933; Cerro Chinguela, 5 km NE Zapalache, LSUMZ 26925–26927; Machete on Zapalache Carmen trail, LSUMZ 26928–26929 (**er-6**). San Martín, Puerto del Monte, 30 km NE los Alisos, LSUMZ 27280–27281 (**er-7**). Huánuco, Unchog, pass between Churubamba and Hacienda Paty, NNW Acomayo, LSUMZ 28167–28168, 28173, 28179–28180, 28182, 28185–28188 (**er-8**).

Sturnira lilium: SURINAM: Marowijne, Oelemarie, TTU-TK 21008 (**li-2**). PERU: Cajamarca, Limón, W of Balzas, FMNH 128837–128839 (**li-3**); Río Zaña, 2 km N Monteseco, FMNH 128856, 128858, 128888–128889, 128891–128892, 128894 (**op-5**). Amazonas, 19 km (by road) E Balzas, FMNH 128812 (**li-1**). Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128814, 128819–128820, 128823, 128825, 128829 (**li-4**); Río Cenepa, vicinity of Huampaní, MVZ 154839–154841; ca. 0.5 mi W of Huampaní, Río Cenepa, MVZ 153362–153365 (**op-6**).

*Sturnira ludovici**: COLOMBIA: Huila/Cauca, 1 mi S Moscopas, Río La Plata, USNM 483510. Magdalena, Sierra Negra, Villanueva, Valledupar, USNM 281259–281261, 281264. Valle del Cauca, Dapa, 15 km NW Cali, USNM 483511; 2 km S de Pance, ca. 20 km SW Cali, USNM 483512–483516. ECUADOR: Cañar, San Jose, 12 mi SW Huicra, FMNH 48785; San Juan, 15 mi W Huicra,

FMNH 48786. Carchi, Maldonado, EPN 7975. Esmeraldas, ca. Río Cauce, FMNH 44296–44297. Pichincha, Gualea, W side Pichincha, AMNH 67329. Loja, Santa Barbara, EPN 2485. Near Mindo, FMNH 48343–48348, 48784; Zapadores, USNM 513448–513449. Pastaza, Mera, USNM 548146; 1.5 km E Mirador, USNM 513456–513457. Imbabura, Paramba, USNM 113370. Zamora-Chinchipe, 3 km NE Cumbaratza, USNM 513452–513455; 4 km NE Sabanilla, USNM 513451. VENEZUELA: Barinas, Altamira, 2 km SW of La Vega del Río Santo Domingo, USNM 440134–440148. Carabobo, San Esteban, FMNH 29440. Distrito Federal, Caracas, 5 km N of Los Venados, USNM 370374–370387, 370389.

Sturnira luisi: PERU: Lambayeque, Las Juntas in Quebrada La Pachinga, ca. 14 km N, 25 km E Olmos, LSUMZ 27256–27257 (**lu-1**); 16 km N, 25 km E Olmos*, MVZ 135569. Piura*, 15 road km E Canchaque, LSUMZ 18982.

Sturnira magna: PERU: Amazonas, ca. 0.5 mi W of Huampaní, Río Cenepa, MVZ 153368–153369, 153371–153372 (**ma-1**). Loreto, Quebrada Orán, 5 km N Río Amazonas, 85 km NE Iquitos, LSUMZ 28288–28289, 28260–28262 (**ma-2**).

*Sturnira mordax**: COSTA RICA: Cartago, Rio Chitaria (above highway), LSUMZ 12788. San José, Fila La Maquina, 7.5 km E Canaan, LSUMZ 12784–12787; Colorado, LSUMZ 11454–11456; San Gerardo, LSUMZ 12781, 12783. Puntarenas, Finca Las Cruces, 2 km S San Vito, FMNH 124092.

*Sturnira nana**: PERU: Ayacucho, Huanhuachayo, AMNH 219138, 219171–219173; LSUMZ 16522–16524, 15683; Río Santa Rosa, San Jose, LSUMZ 16519.

Sturnira oporaphilum: PERU: Amazonas, 3 km E Balzas, FMNH 128919 (**op-1**); Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128920–128925 (**op-2**). Cajamarca, 2 km N of Monteseco, Río Zaña, FMNH 128926–128934, 128795 (**op-3**). BOLIVIA: Santa Cruz, San Rafael de Amboro, MSB 55904, 56184–56185; 4.5 km N, 1.5 km E Cerro Amboro, Río Pitasana, MSB 56177–56178 (**op-4**).

*Sturnira thomasi**: LESSER ANTILLES: Guadaloupe Basse Terre, Grande Etang, AMNH 234950. French Leeward Ids., USNM 361883.

Sturnira tildae: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2128 (MZUSP uncatalogued) (**ti-1**). PERU: Ucayali, Balta, Río Curanja, MVZ 136449, 136487–136489. SURINAM: Marowijne, Oelemarie, TTU-TK 21007. Saramacca, Tafelberg, SE side Arrowhead Basin, TTU-TK 17702, 17703. TRINIDAD: Mayaro, 1 mi S, 2 mi W Guayaguayare, TTU-TK 25221 (**ti-2**).

Sturnira sp. A*: ECUADOR: Chimborazo, Pallatanga, EPN E-6722.

Uroderma bilobatum†: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2107, 2158, 2182, 2198, 2210, 2215, ALG 14924 (MZUSP uncatalogued).

Vampyrops dorsalis†: PERU: Amazonas, 19 km (by road) E Balzas, FMNH 129133–129134, 129137–129138. Cajamarca, Limón, W of Balzas, FMNH 129143 (**vd-1**).

Comparative Morphology of the Glans Penis in *Molossus, Promops,* and *Eumops* (Chiroptera: Molossidae)

JAMES M. RYAN[1]

ABSTRACT

The morphology of the glans penis is described for three genera of molossid bats: *Molossus, Eumops,* and *Promops.* The glans penis in molossids is stout and elongate. Proximally recurved epithelial spines cover the glans penis of all species studied, except species of *Eumops.* The corpora cavernosa are fused and extend well into the glans penis. An os penis is present at the terminus of the corpora cavernosa in all species of *Molossus* and two species of *Eumops (E. auripendulus* and *E. bonariensis*). The corpus spongiosum, which surrounds the urethra, is reduced or absent from the glans penis of molossids. Accessory cavernous tissue is present in the glans but, unlike the corpora cavernosa, is not enclosed in a tunica albuginea. The external morphology of the glans varies remarkably between species. The complex glans penis of molossid bats differs from the simple bulbous glans penis in vespertilionids and emballonurids.

INTRODUCTION

Analysis of the morphology of the reproductive tract, especially the glans penis, has often revealed valuable phylogenetic characters (Bradley and Schmidly, 1987; Breed, 1986; Carleton, 1980; Hooper, 1958, 1959, 1960, 1962; Hooper and Musser, 1964; Lidicker and Brylski, 1987; Morrissey and Breed, 1982; Prasad, 1957; Voss and Linzey, 1981). To date, the vast majority of these studies have cataloged variation in phallic morphology of rodents. Studies of other mammalian orders include those of Short (1979) and Hershkovitz (1979) for primates; Krutzsch and Vaughn (1955), Martin and Schmidly (1982), and Smith and Madkour (1980) for bats; and Walton (1960) for artiodactyls. That the morphological features of the mammalian phallus have evolved rapidly and divergently is not disputed. The cause, however, of this rapid diversification has not been conclusively established (Eberhard, 1985, and Patterson and Thaeler, 1982, notwithstanding).

Despite the value of penile characters for phylogenetic reconstruction in rodents, and the numerous anatomical descriptions of the phallus in the Chiroptera (Brown, 1967; Harrison, 1982; Krutzsch and Crichton, 1987; Matthews, 1937, 1941; Murthy, 1979, 1981; Murthy and Vamburkar, 1978; Wimsatt and Kallen, 1952; Zubaid and Davison, 1987), few studies have used chiropteran penile characters to test phylogenetic hypotheses. In part, this is because the extent of interspecific variation of the chiropteran phallus has not been fully appreciated.

The Molossidae is distributed worldwide and was recently revised by Freeman (1981), who included 12 genera in her classification based on a multivariate analysis of 76 morphometric characters (fig. 1). The present study focuses on phallic variation of *Eumops, Promops,* and *Molossus,* which according to Freeman (1981) are the most highly derived members of a large clade containing eight genera (fig. 1). The purpose of this study is

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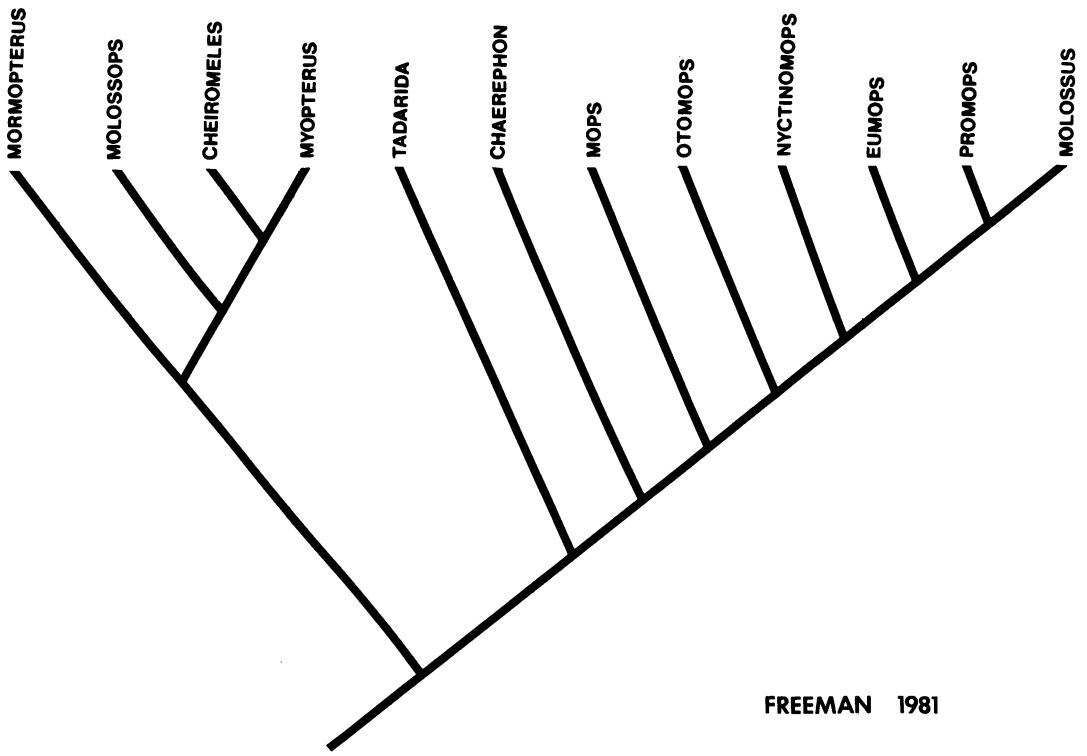

Fig. 1. Phylogeny of the Molossidae based on the 76 morphometric characters analyzed by Freeman (1981).

to describe the morphological variation in the glans penis of these three molossid genera and to demonstrate that sufficient variation exists in the molossid phallus to provide additional systematic characters useful in testing hypotheses of molossid relationships.

Materials and Methods

This study is based on fluid-preserved specimens belonging to the following institutional collections: The American Museum of Natural History, New York (AMNH); The Field Museum of Natural History, Chicago (FMNH); The Royal Ontario Museum, Toronto (ROM); The University of Massachusetts, Amherst (UMA); and The University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Thirty-two specimens representing 10 species were examined: *Eumops auripendulus* (AMNH 42196, 93780, and 71140), *Eumops bonariensis* (UMMZ 124493, 124494, and 124497; FMNH 116562), *Eumops glaucinus* (FMNH 74272), *Eumops perotis* (FMNH 20984, 116727, and 116731), *Promops centralis* (AMNH 61481 and 178692), *Molossus ater* (UMMZ 115248, 115257, 115258, and 115260), *Molossus bondae* (UMA 2778, 2780, 2782, and 2783), *Molossus coibensis* (UMA 2738–2741), *Molossus molossus* (UMMZ 68605, 68606, and 68608), and *Molossus sinaloae* (UMMZ 55851, 55856, 111704, and 111705).

Specimens were originally fixed in 10% buffered Formalin and subsequently stored in 70% ethanol. The glans penis was removed by first making a longitudinal incision along the entire outer sheath and then reflecting the prepuce to expose the glans. Care was taken to make the final transverse incision proximal to the flexure in the stalk of the corpus penis, thus including the entire distal tract. The glans was measured using a Wild M3 binocular dissecting microscope fitted with an ocular micrometer.

At least one specimen of each species was

prepared for scanning electron microscopy according to the following schedule: overnight washing in water followed by serial dehydration in baths of 30%, 50%, 70%, 85%, 90%, 100%, 100%, and 100% anhydrous acetone. The specimen was then critical-point dried in CO_2 with a Balzers CPD 020 critical-point dryer, mounted on a metal stub, sputter-coated with gold–palladium using a Balzers SCD 040 sputter coater, and viewed in a Hitachi S-530 scanning electron microscope operated at 25 kV. Each specimen was photographed, and several specimens were then sectioned again, recoated with gold, and photographed a second time to reveal the internal anatomy of the glans.

A second specimen of each species was cleared and stained with Alizarin Red S according to the following schedule: the specimen was rinsed overnight in water, transferred to 3% KOH for 8 hours, stained in a saturated solution of Alizarin Red S in 2% KOH for 3 hours, washed in 3% KOH for 2 hours to remove excess stain, and passed through a graded series of KOH/glycerine solutions to 100% glycerine.

Additional specimens were either thick-sectioned with a razor blade and viewed under a Wild M3 dissecting microscope, or embedded in methacrylate, thin-sectioned (1–2 microns), and stained in Toluidine Blue and Basic Fuchsin according to procedures outlined by Humason (1972). Histological sections, thick sections, and cleared-and-stained specimens were used, along with SEM photographs, to clarify the position of internal features. The morphology of the glans penis was then reconstructed from scaled drawings.

TERMINOLOGY: Although the morphology of the glans penis has been described for a diverse assemblage of microchiropteran species, inconsistent terminology and incomplete descriptions have made penile characters of little use to chiropteran systematists (except Smith and Madkour, 1980). In an effort to provide accurate and consistent descriptions of the molossid glans penis and to allow comparisons with other mammalian taxa, it is first necessary to define the limits of the glans penis. In humans, the glans penis is the distal expansion of the corpus spongiosum, covering the blunt ends of the paired corpora cavernosa (Pansky, 1984) and beginning at the junction of the double layer of skin called the prepuce (fig. 2A).

In canids, the glans penis consists of two functional units: the highly vascular bulbus glandis and the distal pars longa glandis. Unlike the condition found in humans, however, the corpora cavernosa are reduced and terminate in a long os penis. The os penis is surrounded by the expanded glans penis and housed within a prepuce attached to the skin of the inguinal wall. The prepuce attaches to the penile shaft at the midpoint of the bulbus glandis (Evans and Christensen, 1979).

In rodents, the glans penis is defined externally as that portion of the penis distal to the attachment of the prepuce with the shaft (Hooper, 1958). However, defining the limits of the glans penis in molossid bats is problematic. The traditional human and canine definition—a distal expansion of the corpus spongiosum—is inappropriate for molossids because the distal corpus spongiosum is not greatly expanded (fig. 2B).

Here I choose to follow Hooper (1958) and Smith and Madkour (1980) in defining the chiropteran glans penis as that part of the penis distal to the glans–prepuce junction. In general, terminology follows Hooper (1958), Smith and Madkour (1980), and Wimsatt and Kallen (1952).

ACKNOWLEDGMENTS

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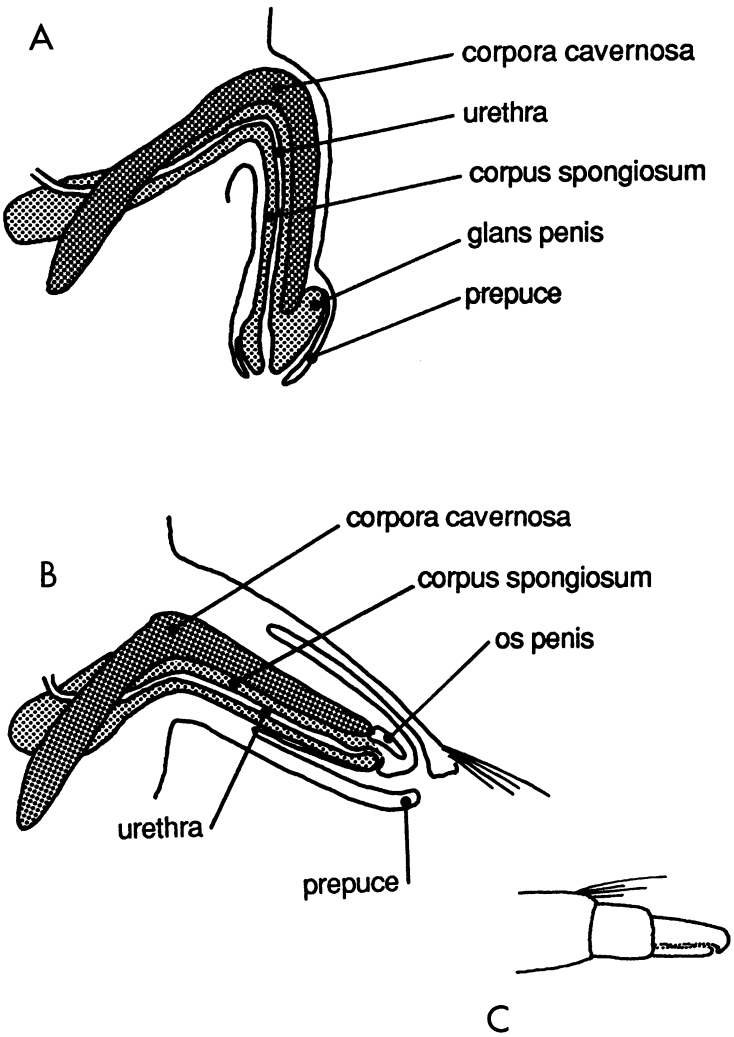

Fig. 2. Lateral views of the internal structure of the penis. **A.** Human. **B.** Molossid bat with the glans penis retracted within the prepuce. **C.** Molossid bat with an erect glans penis, showing the glans extended beyond the everted prepuce.

liam Bemis (University of Massachusetts) for the use of his laboratory and equipment for the histological preparations. Finally, I thank Karl Koopman for his lifetime contribution to the study of bats. Funding for this project was provided by a Faculty Research Grant from Hobart and William Smith Colleges.

DESCRIPTION OF PHALLI

Externally, the body of the molossid penis is enclosed in a hairy pendulous sheath (fig. 2B). The prepuce is a thin cylindrical layer of epithelium attached to the base of the glans and to the distal rim of the thick outer sheath. When erect, the glans penis extends beyond the outer prepucial sheath (fig. 2C). The outer sheath is covered with short hairs except along its dorsal rim, where a tuft of long, stiff hairs is found. The function of these hairs is unknown, but they appear to project from a small prepucial gland.

Molossus Species

EXTERNAL ANATOMY: The description that follows is based on *M. ater*. Only differences

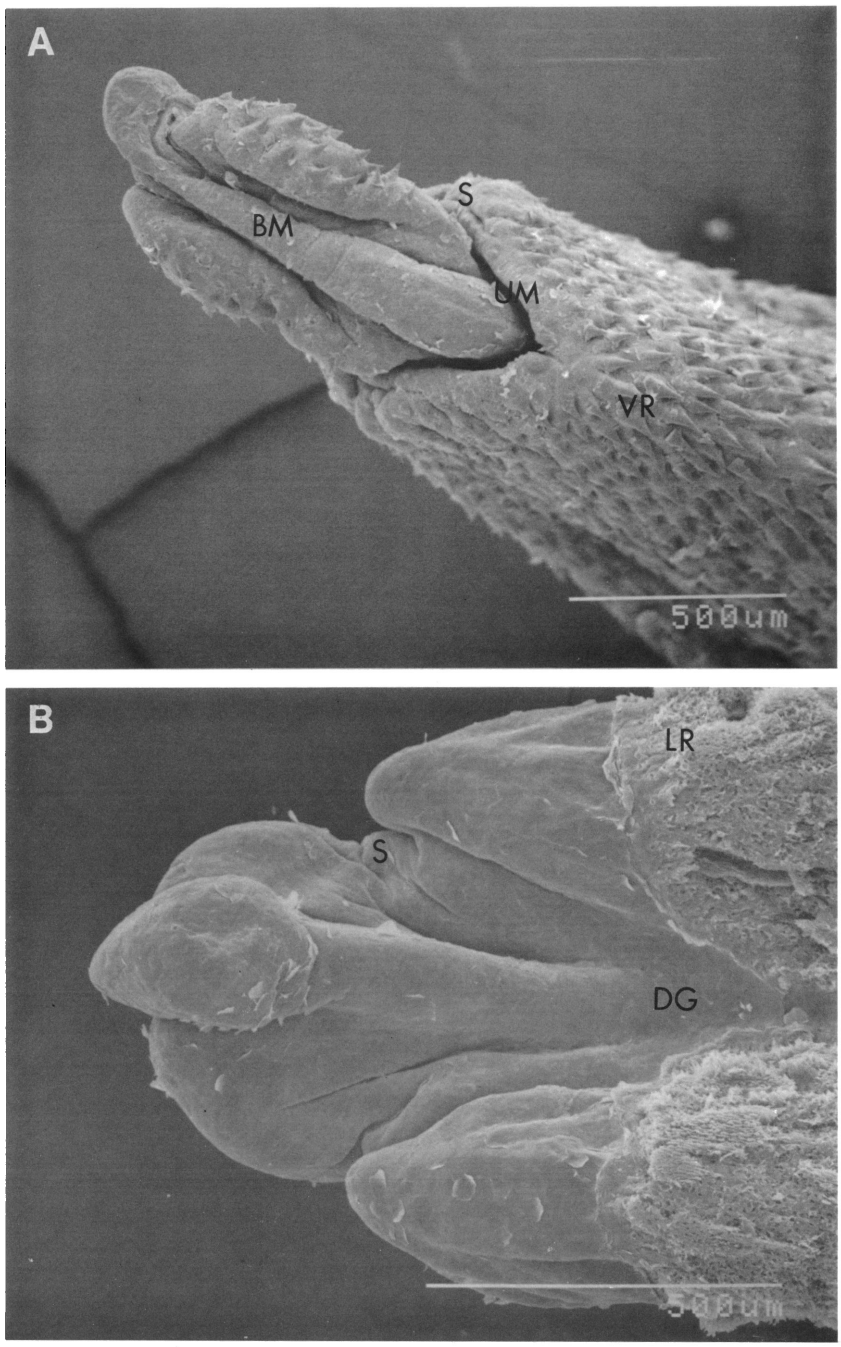

Fig. 3. **A.** Ventral view of the distal glans penis of *Molossus ater*. **B.** Dorsal view of the bacular mound in *M. sinaloae*. BM, bacular mound; DG, dorsal groove; LR, lateral ridge; S, subapical constriction; UM, urinary meatus; VR, ventromedial ridge.

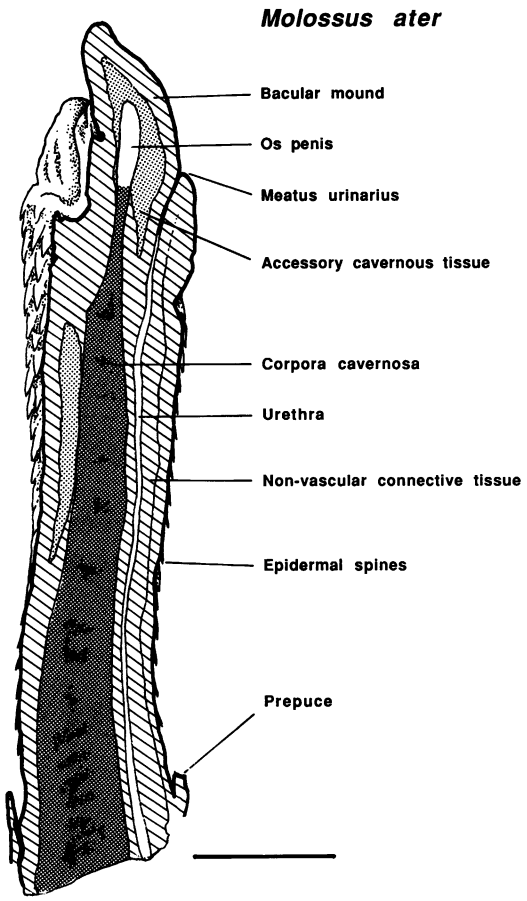

Fig. 4. Sagittal section through the glans penis in *Molossus ater*. Distal is toward the top of the page and ventral to the right. Scale bar = 500 μm.

TABLE 1
Dimensions (in millimeters) of the Glans Penis in Selected Species of *Molossus*

Specimen	Glans length	Greatest glans width	Tip length	Tip width
M. ater				
UMMZ 115258	5.6	2.0	0.9	0.6
UMMZ 115248	5.5	2.4	0.9	0.7
UMMZ 115260	5.7	2.1	0.7	0.8
M. bondae				
UMA 2782	5.2	1.9	0.7	0.6
UMA 2780	5.0	1.9	0.7	0.6
UMA 2778	4.9	1.8	0.7	0.55
M. coibensis				
UMA 2738	4.7	1.7	0.5	0.55
UMA 2739	4.6	1.9	0.6	0.5
UMA 2741	4.1	1.9	0.4	0.5
M. molossus torpidorhyncus				
UMMZ 68605	3.2	1.0	0.6	0.5
UMMZ 68608	3.5	1.1	0.4	0.5
M. sinaloae				
UMMZ 111704	3.0	1.4	1.0	0.5
UMMZ 55851	2.9	1.2	0.5	0.4
UMMZ 111705	3.0	1.5	0.6	0.5
UMMZ 55856	3.0	1.3	0.5	0.6

from *M. ater* will be described for the other four species.

The glans penis in *M. ater* is the largest of all molossid species studied here (table 1). The glans is cone-shaped, tapering gently to the subapical constriction at the level of the urinary meatus (fig. 3). Distal to the urinary meatus, a prominent spear-shaped bacular mound (0.7–0.9 mm long) contains the small os penis. Along the ventral surface of the glans, a large medial ridge encloses the urethra. Paired lateral ridges flank the medial ridge and terminate at the subapical constriction. The dorsal surface of the glans is rounded at its base. At midlength, a middorsal groove widens distally and becomes continuous with the bacular mound.

A narrow medial ridge extends from (and forms the dorsal wall of) the urinary meatus to the apex of the bacular mound and terminates on the middorsal surface of the mound (figs. 3, 4). Lateral to this ridge are paired semicircular lobes covered with small proximally recurved spines of keratinized epithelium. The outer surface of the glans is covered with larger proximally recurved spines, which become smaller distally (fig. 5). The rim of the urinary meatus, the middorsal groove, and the medial part of the bacular mound lack spines.

In general, there appears to be little morphological variation (except size) among the species of *Molossus* studied here (table 1). The middorsal groove extends nearly to the glans–prepuce junction in *M. coibensis*, and as in *M. bondae* is smaller in overall proportion. Spines are absent (or highly reduced) from the lateral semicircular lobes of the bacular mound in *M. coibensis*, *M. molossus*, and

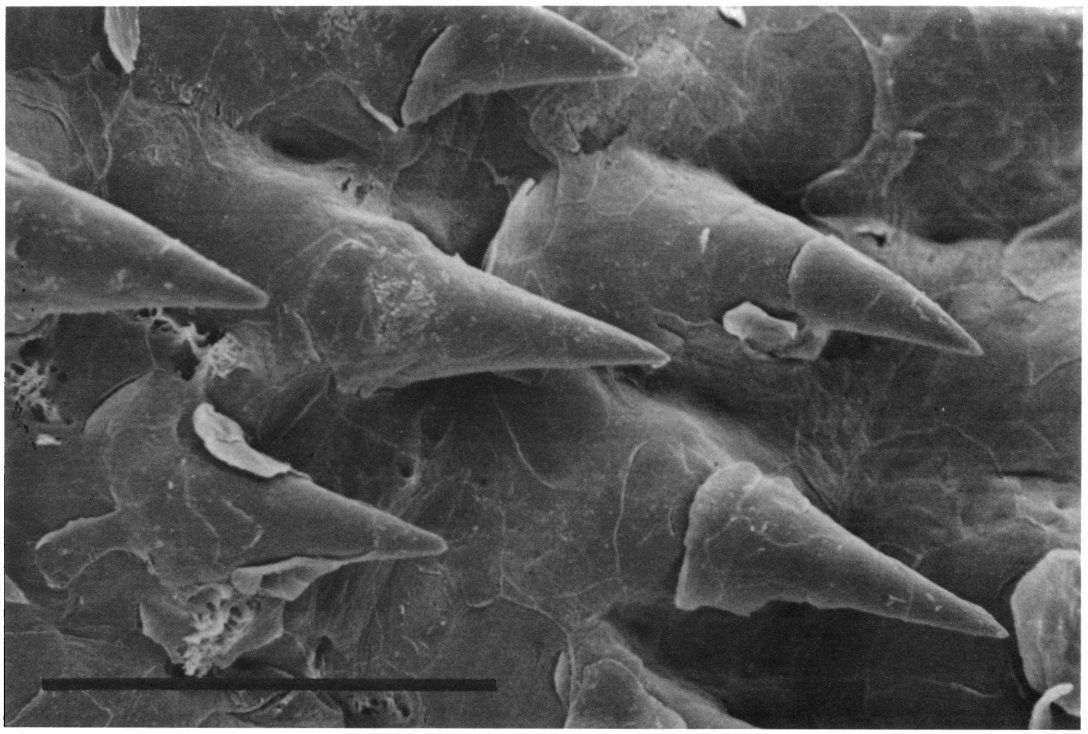

Fig. 5. Epidermal spines along the shaft of the glans penis in *Molossus ater*. Scale bar = 100 μm.

M. sinaloae. The glans penis is smallest in *M. molossus* (table 1), being approximately 3 mm in length.

INTERNAL ANATOMY: Internally, the microchiropteran glans penis is markedly different from that found in humans. In humans, the corpora cavernosa are restricted to the corpus penis and do not enter the glans. Rather, the glans is formed from a distal expansion of the corpus spongiosum (Pansky, 1984). In many Microchiroptera, the corpora cavernosa extend well into the glans penis and the corpus spongiosum is reduced to a thin layer surrounding the urethra (Matthews, 1941; Smith and Madkour, 1980).

In *M. ater,* the paired cylindrical corpora cavernosa are the main vascular tissue in the glans penis (figs. 4, 6). They extend distally, forming the dorsum and sides of the penis. Along the ventral (urethral) midline of the fused corpora cavernosa is a groove supporting the corpus spongiosum and urethra. The corpora cavernosa are fused at the base of the glans (fig. 6B) and are surrounded by the thick-walled tunica albuginea. Medially, a thin dorsoventral septum separates the corpora cavernosa. The corpora cavernosa are made of loose connective tissue or trabeculae (trabeculae corporum cavernosum). These fibroelastic and muscular tissue bands traverse the interior of the corpora cavernosa, forming numerous vascular sinuses or lacunae. During erection, these sinuses fill with blood that stretches the surrounding tunica albuginea and stiffens the shaft.

The os penis is *Molossus* species is relatively small (Brown, 1967). Smith and Madkour (1980) suggested that the os penis is derived from the corpora cavernosa and that reduction of the os penis results from deossification in this region. Reduction or loss of the os penis is probably the derived condition for bats (Smith and Madkour, 1980). The os penis in *M. ater* is small (300 microns) and slightly wider at the base. It is embedded in the medial ridge of the bacular mound.

The corpus spongiosum is a second vascular tissue surrounding the urethra. The tu-

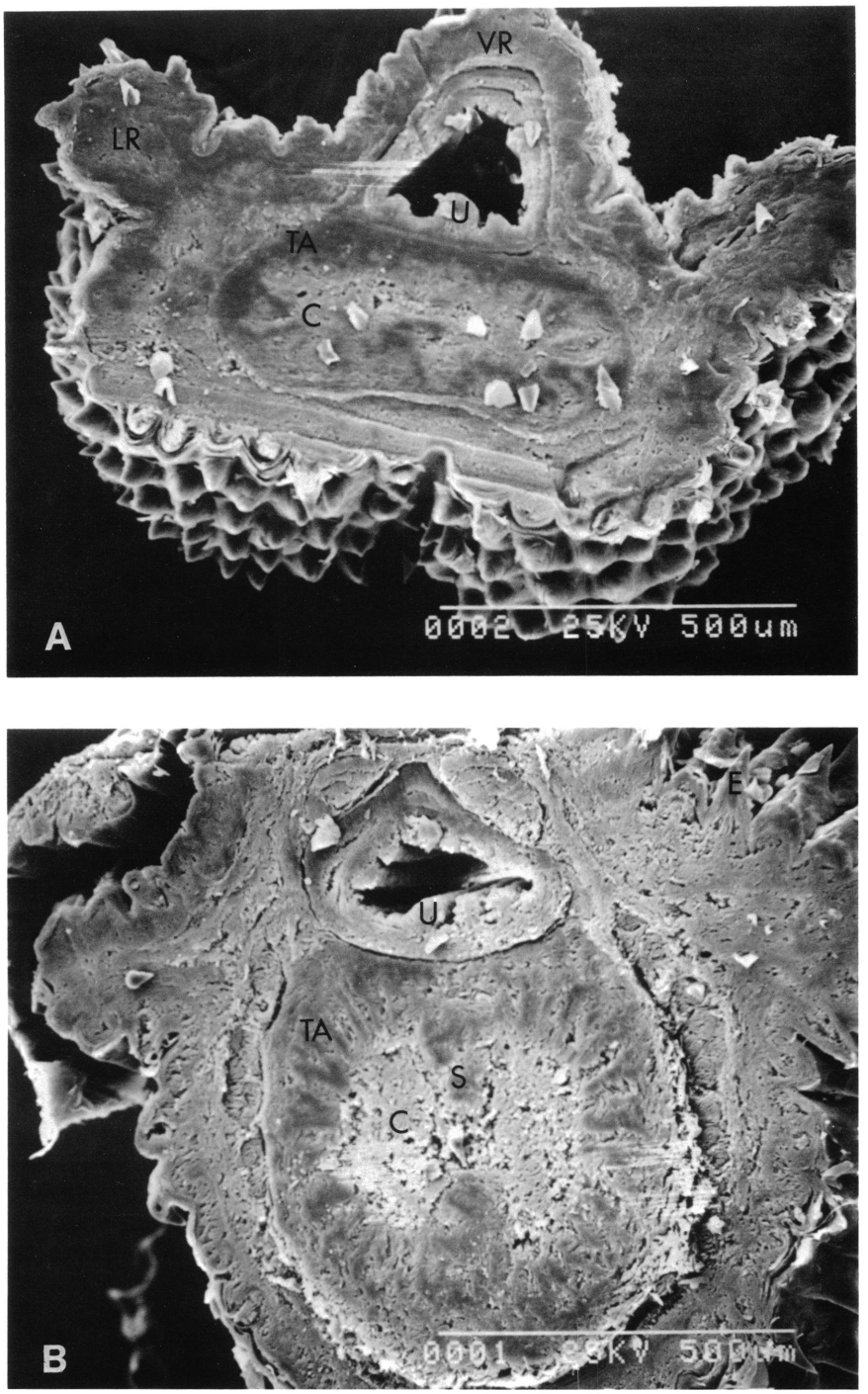

Fig. 6. Transverse sections through the glans penis of *Molossus ater*. **A.** Section through the glans ventral to the subapical constriction. **B.** Section through the glans near the glans–prepuce junction. C, corpora cavernosa; E, epithelial spines; LR, lateral ridge; S, septum of the tunica albuginea; TA, tunica albuginea; U, urethra; VR, ventromedial ridge.

nica albuginea of the corpus spongiosum is considerably thinner and more elastic than that of the corpora cavernosa. It is present in the proximal glans in molossids, but becomes reduced distally (fig. 6); a condition considered primitive for mammals (Smith and Madkour, 1980).

In many bats, but not in primates, a third vascular tissue—the accessory cavernous tissue (Smith and Madkour, 1980)—contains large trabecular sinuses not enclosed within a tunica. Accessory cavernous tissue is restricted to the distal two-thirds of the glans in molossids (fig. 4), where it surrounds the distal corpora cavernosa and os penis. In vespertilionids, the accessory cavernous tissue invades the prepuce (Wimsatt and Kallen, 1952). In *M. ater,* some accessory tissue is found dorsal to the corpora cavernosa at midglans and a second sinus is located in the bacular mound (fig. 4). Presence of accessory cavernous tissue in the glans penis is believed primitive for mammals (Smith and Madkour, 1980).

In *M. ater,* the urethra lies within a pronounced ventromedial ridge (figs. 3, 6) and exits the glans at the urinary meatus on the ventral surface of the glans at the subapical constriction. I noted little variation in the internal anatomy of the glans in the other species of *Molossus.* Brown (1967) detailed the bacular variation in 12 species of *Molossus* and observed a great deal of intraspecific variation in size and shape.

Eumops Species

EXTERNAL ANATOMY: The glans penis of *E. bonariensis* is considerably smaller (1.5–2.5 mm) than that of *M. ater.* The glans is oval at its base and widens distally to form three prominent lobes: two lateral and one dorsal (figs. 7A, 8). The two lateral lobes join along the ventral midline, creating a V-shaped furrow that terminates at the urinary meatus at the base of the bacular mound (fig. 7A). A bulbous bacular mound protrudes from the ventral surface of the dorsomedial lobe and forms the dorsal rim of the urinary meatus (fig. 8). The oval-shaped bacular mound extends slightly further distad than the rim of the dorsal lobe. The outer surface of the glans penis in *E. bonariensis* is devoid of epithelial spines (fig. 7A).

The glans penis of *E. auripendulus* is distinct from that of its close relative *E. bonariensis* (figs. 7B, 9). At its base the glans is oval in cross section, but at midlength the glans widens and is dorsoventrally compressed. From its widest point (approximately two-thirds the distance from the prepucial junction) the glans tapers sharply and terminates bluntly. Along the ventral surface of the glans there is a prominent medial ridge that encloses the uretha (fig. 7B). This urethal ridge terminates by forming a collar around the vental rim of the urinary meatus. On the ventral surface of the glans tip there is an oval bacular mound. The mound is not as pronounced as in *E. bonariensis,* but it does enclose a small os penis and forms the dorsal margin of the urinary meatus (fig. 9). As on the glans penis of *E. bonariensis,* epithelial spines are absent from the glans penis of *E. auripendulus.* The glans penis of *E. glaucinus* and of *E. perotis* does not differ significantly from that of *E. auripendulus.*

INTERNAL ANATOMY: As in other molossids, the fused corpora cavernosa terminate near the midpoint of the glans penis (figs. 8, 9). The corpora cavernosa are surrounded by the thick-walled tunica albuginea and, as in species of *Molossus,* an incomplete septum is found where the two corpora cavernosa have fused medially.

Not all species of *Eumops* have an os penis. Brown (1967) was unable to find an os penis in *E. perotis* and *E. trumbulli.* In those species that do possess an os penis, there is considerable variation in its size and shape. It is large and curved in *E. bonariensis,* but small and straight in *E. auripendulus.* The os penis tapers gently to end in a blunt tip. The tip of the os penis lies within the bacular mound distal to the urinary meatus (figs. 8, 9) except in *E. auripendulus,* where it barely enters the bacular mound (fig. 9).

Some accessory cavernous tissue is present in all species of *Eumops* examined. The urethra enters the glans along its ventral surface and is surrounded by a thin corpus spongiosum. The urinary meatus lies proximal to the bacular mound (figs. 8, 9).

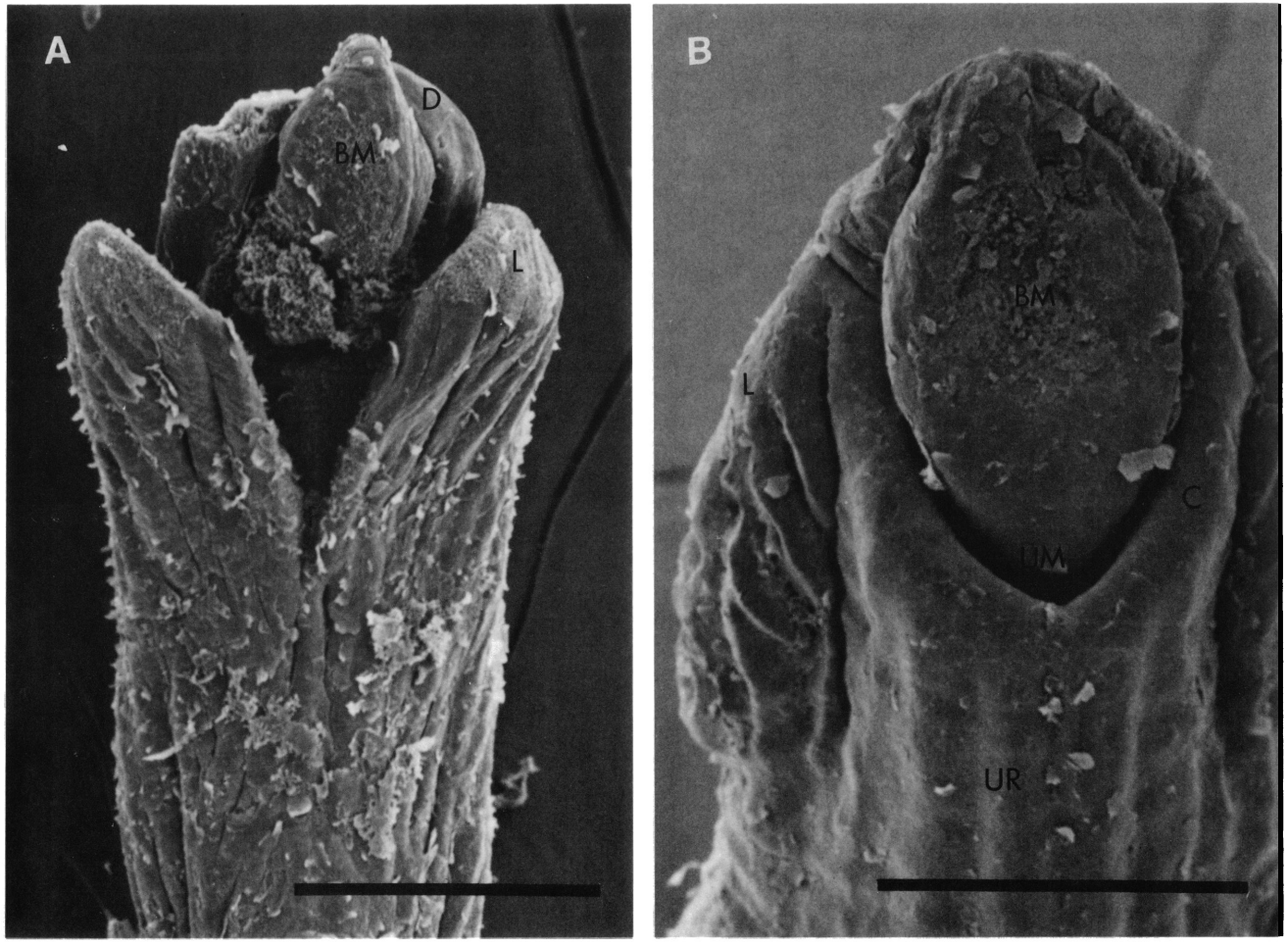

Fig. 7. Ventral views of the glans penis. **A.** *Eumops bonariensis.* **B.** *E. auripendulus.* BM, bacular mound; C, urethral collar; DL, dorsal lobe; F, central furrow; LL, lateral lobe; UM, urinary meatus; UR, urethral ridge. Scale bar = 500 μm.

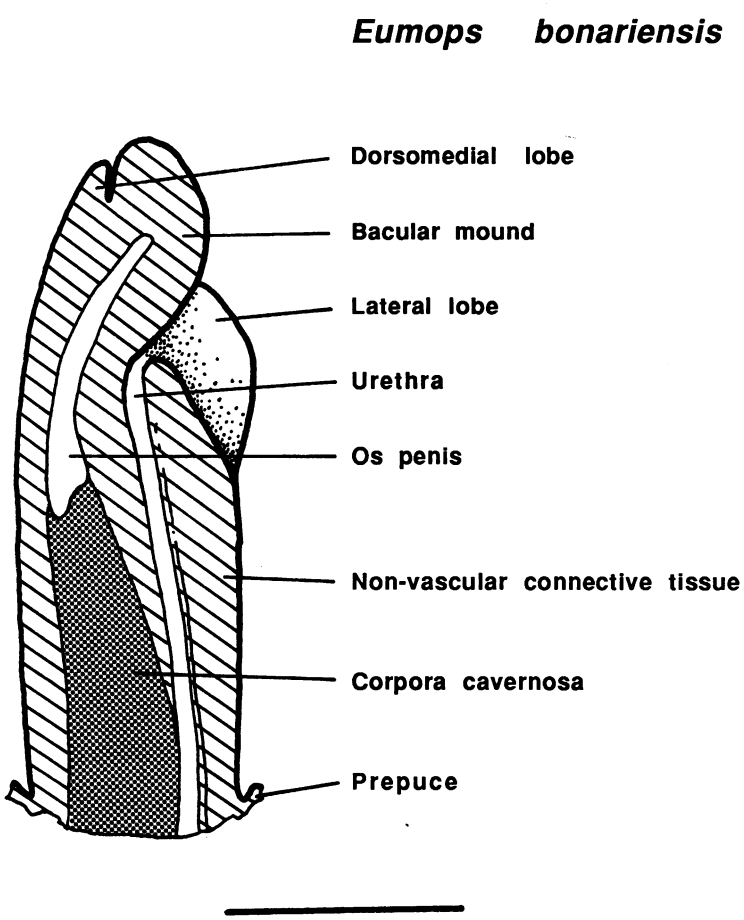

Fig. 8. Sagittal section through the glans penis of *Eumops bonariensis*. Distal is toward the top of the page and ventral to the right. Scale bar = 500 μm.

Promops centralis

EXTERNAL ANATOMY: The glans penis of *P. centralis* (fig. 10) is stout and long (approximately 4 mm long) and superficially resembles the much smaller glans of *E. auripendulus*. The glans is dorsoventrally compressed throughout its length. A urethral ridge runs along its ventral midline and terminates at the base of the bacular mound. The urinary meatus is crescent-shaped and bordered dorsally by the caudal surface of the bacular mound and ventrally by a thick collar formed where the urethral ridge ends (fig. 10). Unlike that of *E. auripendulus*, the glans penis of *P. centralis* is covered with large proximally recurved spines. Spines are absent from the urethral collar and the ventral surface of the bacular mound (fig. 10).

INTERNAL ANATOMY: The glans penis of *P. centralis* lacks an os penis (also see Brown, 1967). The fused corpora cavernosa continue to the base of the bacular mound at the level of the urinary meatus. Instead of an os penis, the bacular mound contains a mixture of connective tissue and accessory cavernous tissue (fig. 11). Although the accessory cavernous tissue contains fewer trabeculae, some enlargement or swelling of the bacular mound is likely during erection.

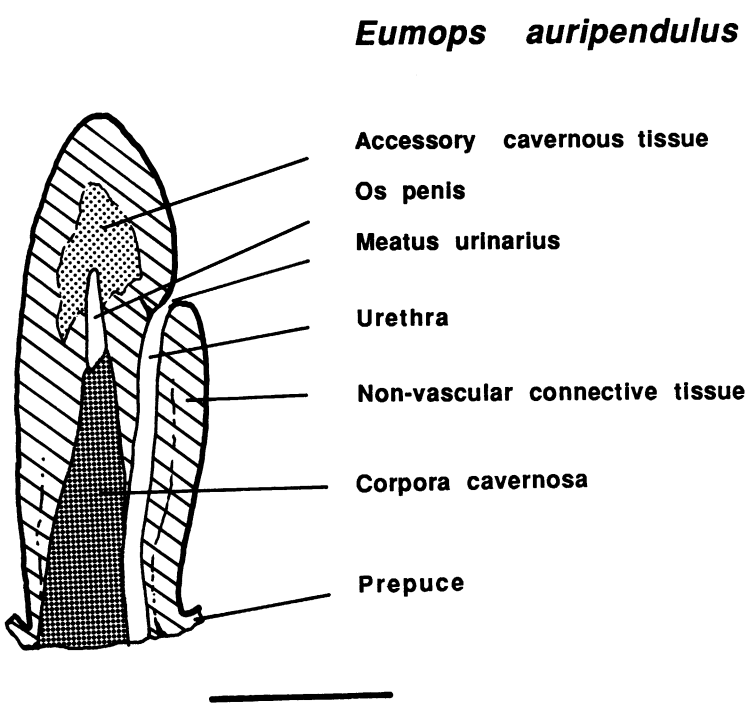

Fig. 9. Sagittal section through the glans penis of *Eumops auripendulus*. Distal is toward the top of the page and ventral to the right. Scale bar = 500 μm.

DISCUSSION

Although a comprehensive survey of the anatomy of the glans penis in molossid bats is lacking, sufficient descriptions now exist to reveal extensive interspecific variation and to indicate several traits common to the family. First, the molossid glans penis is elongate and conical, not short and bulbous as in vespertilionids and emballonurids (Matthews, 1941; Wimsatt and Kallen, 1952). Second, the prepuce is thin and retractile, being only loosely connected to the underlying tissue of the outer sheath. This condition contrasts sharply with the thick glandular prepuce of vespertilionids (Wimsatt and Kallen, 1952). During erection, the molossid glans swells and is forced craniad, out of the outer sheath, so that the glans is visible externally. The swelling is caused by blood filling two vascular tissues: corpora cavernosa and accessory cavernous tissue. The fused corpora cavernosa extend well into the glans penis in molossids, and when the trabecular spaces of the corpora cavernosa fill with blood the glans becomes erect. Corpora cavernosa do not enter the glans penis in vespertilionids (or humans), and the presence of these fused vascular tissues within the glans is probably primitive (Smith and Madkour, 1980). Accessory cavernous tissue, although present in all molossids examined in this study, is not extensive in the three genera studied here, relative to the genera *Molossops* and *Mormopterus* (personal obs.). The corpus spongiosum, a third vascular tissue that composes the bulk of the glans penis in humans, is poorly developed in molossids and many other bats (Matthews, 1941). This tissue, which surrounds the urethra, is present in the corpus penis but rarely penetrates far into the glans.

The os penis lies at the terminus of the fused corpora cavernosa and is thought to be a distal ossification of that tissue (Smith and Madkour, 1980). Reduction or loss of the os penis is considered the derived condition for bats (Smith and Madkour, 1980). In the Molossidae studied here, the os penis is present

Fig. 10. Ventral view of the glans penis of *Promops centralis*. BM, bacular mound; C, urethral collar; UM, urinary meatus; UR, urethral ridge. Scale bar = 500 μm.

in three species of the genus *Eumops* and all species of *Molossus,* but is absent from *Promops*. If the os penis is an important phylogenetic character, as others have suggested (Brown, 1967), then this sporadic distribution of the os penis in molossids is problematic. According to Freeman (1981), *Eumops* is the sister group of *Promops* and *Molossus*. However, this requires the independent loss of the os penis at least twice, once in several species of *Eumops* and a second time in *Promops*.

The possession of epidermal spines or similar ornamentation presents a similar problem. Epidermal spines are found in most molossids, including *Mormopterus, Molossops,*

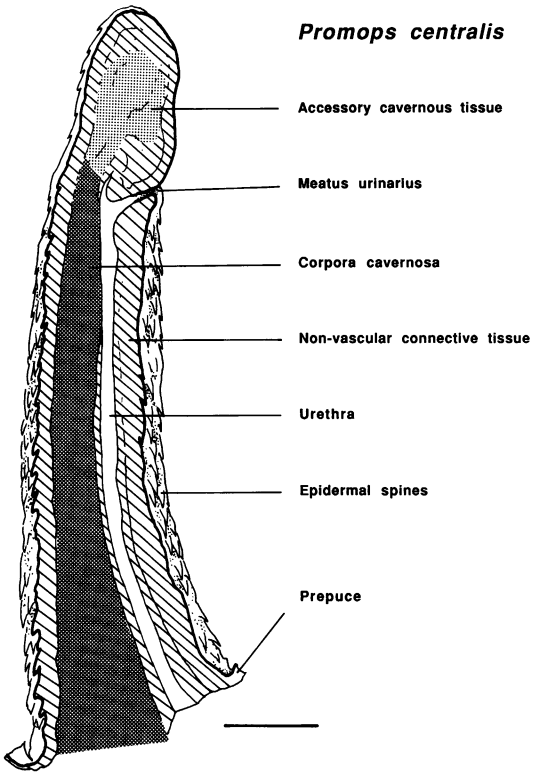

Fig. 11. Sagittal section through the glans penis of *Promops centralis*. Distal is toward the top of the page and ventral to the right. Scale bar = 500 μm.

Tadarida, Promops, and *Molossus* (personal obs.). However, they are absent from species of *Eumops*. Members of the genus *Eumops* also possess another uniquely derived character among molossids: a short glans penis. In fact, a great deal of interspecific variation occurs within the genus *Eumops*. Whereas *E. auripendulus, E. glaucinus,* and *E. perotis* share similar glans structure, the glans of *E. bonariensis* is quite different (fig. 7). Analysis of the glans penis does not support Freeman's (1981) claim that *E. bonariensis* is phenetically closely related to *E. underwoodi, E. glaucinus,* and *E. maurus*.

The phallus has already proven useful in addressing higher-level taxonomic questions, such as the supposed diphyly of the Chiroptera (Smith and Madkour, 1980). In addition, Matthews (1937, 1941) described the anatomy of the phallus for representatives of six Old World microchiropteran families: Rhinolophidae, Nycteridae, Megadermatidae, Emballonuridae, Hipposideridae (considered a subfamily of rhinolophids by Koopman, 1984), and Vespertilionidae. He recognized two general types of glans penis: those with a small bulbous glans and thick glandular prepuce (vespertilionids and emballonurids) versus those with an elongate, structurally complex glans and thin retractile prepuce (rhinolophids, nycterids, megadermatids, and now molossids). The occurrence of two basic penile morphs within Chiroptera is reminiscent of the simple versus complex penis dichotomy of New World muroid rodents (Carleton, 1980; Hooper and Musser, 1964). However, molossids and vespertilionids are both members of the infraorder Yangochiroptera (Koopman, 1984) yet exhibit opposing penile morphologies. Thus, if the two microchiropteran penile morphs represent a true phylogenetic dichotomy, then the infraorders Yinochiroptera and Yangochiroptera may be artificial.

Matthews (1937, 1941) demonstrated extensive interfamilial variation in the microchiropteran glans penis and used this variation to address phylogenetic questions above the family level. The present study uncovers significant interspecific variation in the molossid glans penis. A revision of the Molossidae based on penile anatomy is no doubt premature until representatives from all genera have been examined. However, the chiropteran phallus exhibits striking variation that may prove useful in addressing phylogenetic questions above the generic level as well.

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A Brief History of Bolivian Chiroptology and New Records of Bats

SYNDEY ANDERSON[1]

ABSTRACT

Cumulative numbers of the 100 presently recognized species of bats known from Bolivian specimens are graphed against time, by dates of original description, dates of first Bolivian specimens, and dates of first published reports. Original descriptions accumulated most rapidly in the decades from 1810 to 1870, and 50% of the species now known from Bolivia had been described by 1850. Seventy percent of the first specimens from Bolivia have been obtained since 1960, and 50% have been reported since 1980. In South America, large mammals became known earlier than did bats, and bats earlier than small rodents. This sequence probably occurred for all continents, and the larger geographic ranges of bats than of rodents probably account for the difference in rapidity of discovery between bats and rodents. The first Bolivian records of six species and one subspecies of bats are documented here.

INTRODUCTION

By 1850, about 90% of the presently recognized species of South American mammals larger than a tree squirrel had been named, according to Hershkovitz (1987). He also estimated that only 10% of the small mammals were known by 1850, but the estimate of 90% is somewhat high and that of 10% is somewhat low, as we shall see. However, it is clear that the larger mammals became known sooner.

There are fewer kinds of large mammals and their conspicuousness and economic importance tend to make them more familiar. Furthermore, species of larger mammals tend to have larger geographic ranges than smaller mammals have (Anderson, 1977), and this would have increased the probability of discovery of large mammals.

The times of discovery (as evidenced by their descriptions) for bats and rodents are examined here and compared with times for large mammals in South America, North America, and Australia (figs. 1, 2). Curves of the type shown in figures 1 and 2 were presented for North American birds, and several other major groups, by Steyskal (1965).

Reports of taxa recently discovered in Bolivia are summarized here, including species and subspecies reported here for the first time.

METHODS

Data were extracted from files accumulated since 1980 for a long-term survey of the native mammals of Bolivia. All relevant literature known to me and all specimens known from study of specimens in the major museums holding Bolivian material were used. Much of this information for bats was summarized by Anderson et al. (1982), and several more recent publications have added to our knowledge (Ibañez, 1985; Torres et al., 1988; Ibañez and Ochoa, 1989; Wilson and Salazar, 1990).

For the 100 species of bats now known from Bolivian specimens, the dates of original descriptions (mostly based on specimens from other parts of the Neotropics), the col-

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lection dates of the first Bolivian specimen of each, and the dates of the first published report of each were tallied. The times of discovery of South American large mammals, bats, and small rodents were compared by tallying the decades of original desciptions of the species currently recognized. Data are from Honacki et al. (1982). The sample of large mammals was limited to 110 species of Primates, Carnivora, Perissodactyla, and Artiodactyla (large rodents and edentates were not included); 182 species of bats were used; and the sample of small rodents was limited to the Muridae (212 species).

Acknowledgments

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RESULTS AND DISCUSSION

Three Linnaean (1758) species are among the 100 bats known from Bolivia (fig. 1). As of February 1988, I knew of records of 13 species awaiting publication. By 1850, 50% of the species had been discovered, and 50% of the species (from the 25th to 75th percentiles) were described in the six decades from 1820 to 1880. About 70% of the first Bolivian specimens have been obtained since 1960, and 50% of their reports have been published since 1980.

Cumulative percentages of South American large mammals, bats, and small rodents are plotted for comparison in figure 2. Because more than half (100 of 182) of the South American species of bats occur in Bolivia, the curve for Bolivian bats (in fig. 1) is similar to that for South American bats (in fig. 2). The patterns of discovery for different groups of mammals are quite different. Large mammals in general were discovered earlier: 20% of South American large mammals were described before 1770, and the 50th percentile was reached by about 1815. Bats were next: 3% were described before 1770, and the 50% level was reached by about 1870. The mice and rats were last: the first was not described until 1810, and the 50% level was not reached until about 1905. By 1920 the percentage of murid rodents that had been discovered exceeded the percentage of bats. There are more species of bats than of large mammals, and more murids than bats. The sequence from large mammals to bats and finally rodents is apparent in North American and Australian data that I have compiled and is probably true for other continents as well.

The "break-back" mouse trap came into common use in the late 19th century, and the nylon mist net for bats in the mid-20th century. However, most of the species were discovered without this newer technology. Rodents have smaller geographic ranges than bats, and this reduces the probability for rodents that any given collecting site will fall within the range of a given species. (For data on range sizes see Anderson [1977] and Anderson and Koopman [1981].)

Historical rates of discovery are influenced by various factors, including the amount and location of geographic space explored and numbers of specimens obtained. Techniques for obtaining specimens probably also interacted with the sizes of individuals, species densities in different local faunas, rarity in terms of population densities of species, sizes of geographic ranges, and habits of species to influence the historical rates of discovery.

Factors increasing the probability of discovery of a species are greater space explored, greater biological ignorance of the area selected for exploration, more specimens obtained, more varied techniques for collecting, larger sizes of animals, greater species density, greater population density, and more conspicuous habits (diurnal rather than nocturnal; in open areas rather than concealed places). These variables are not completely independent, and study of their correlations and interactions would be interesting. Among the biological (as distinct from the historical) variables, the most important seems to be range size. At least, I will hypothesize that

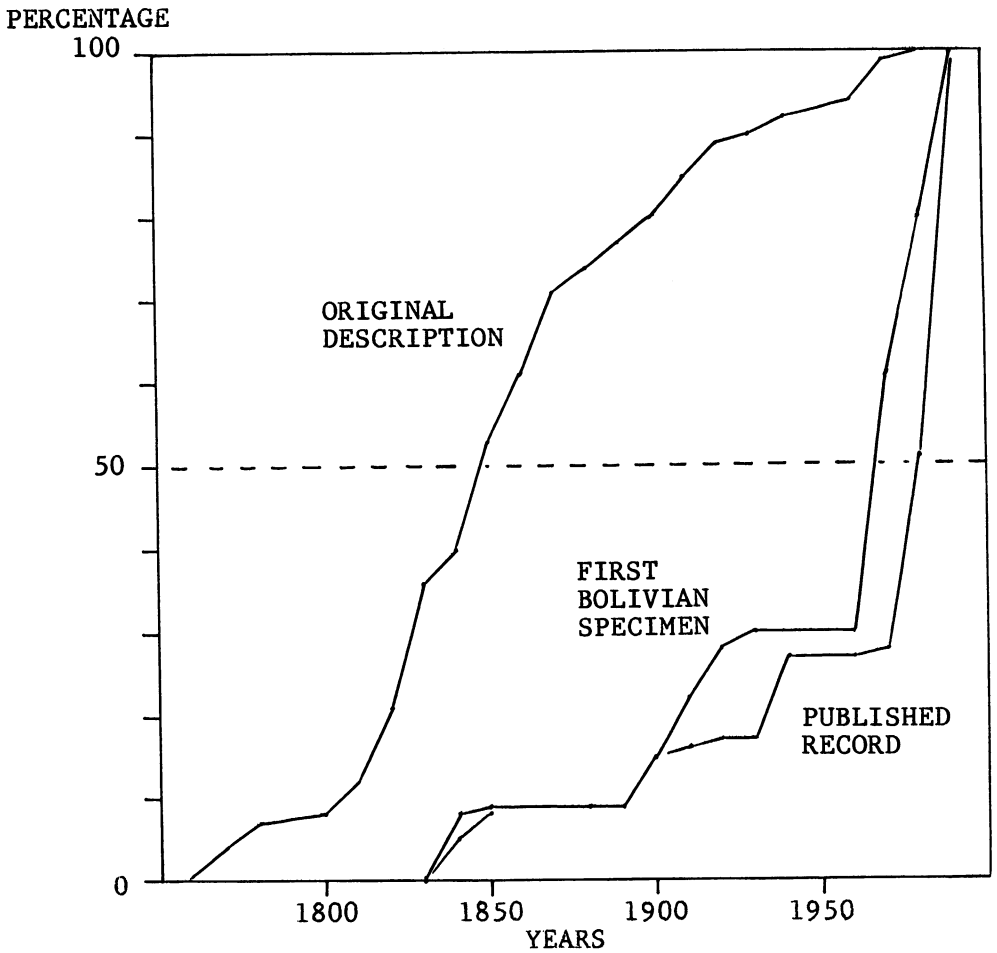

Fig. 1. Graph of cumulative numbers by decades of original descriptions of currently recognized species now known from Bolivia, when the first Bolivian specimens were obtained, and when the first published reports appeared.

the earlier discovery of bats than of rodents is due mainly to the fact that species of bats have larger geographic ranges than do rodents. Although I do not have a set of distribution maps and thus do not have quantitative data on range sizes for South American rodents, such data are available for South American bats and for both bats and rodents of North America and Australia (table 1).

The probability of capture within a continent is a function of the range of a species within that continent. Other things being equal, a species with a range twice as large as another species is twice as likely to be discovered through a given amount of exploratory effort. The probability of discovery is a function of the total range of the species. Inclusion of total ranges in calculating the geometric mean for ranges of species of a given group occurring within a continent may raise the mean appreciably if many species occur also in another continent and if their ranges in that continent are large relative to ranges in the first continent.

Furthermore, those groups that have species with large ranges within a continent will have larger percentages of species occurring also beyond that continent (Anderson, 1977; Anderson and Koopman, 1981). For exam-

TABLE 1
Geometric Means of Range Sizes (in units of 10^5 km^2)

	South America	North America	Australia
Large mammals	20?[a]	25[b]	2.6[c]
Bats	23.4 (26.1)[d]	7.7 (23.4)[d]	5.1
Rodents	3?[a]	1.8	2.1

[a] A predicted value, not measured.
[b] Carnivora, Perissodactyla, and Artiodactyla (ranges within North America only).
[c] Marsupialia (only about half of which are large).
[d] Range size within the continent and (in parentheses) total range size when that part of each range in the other American continent is added.

ple, bats and birds (Anderson, 1984) have relatively large ranges and rodents have small ranges. Of 140 North American bats occurring, at least in part, north of Nicaragua, 82 (58%) occur also in South America. In comparison, of 372 North American rodents occurring north of Nicaragua, 9 (2.4%) occur also in South America.

Bats are more abundant as individuals and as species in tropical than in temperate areas, and South America has more tropical terrain than North America. Consequently, as shown by the data in table 1, the addition of the extracontinental parts of ranges for species occurring in both continents to the ranges

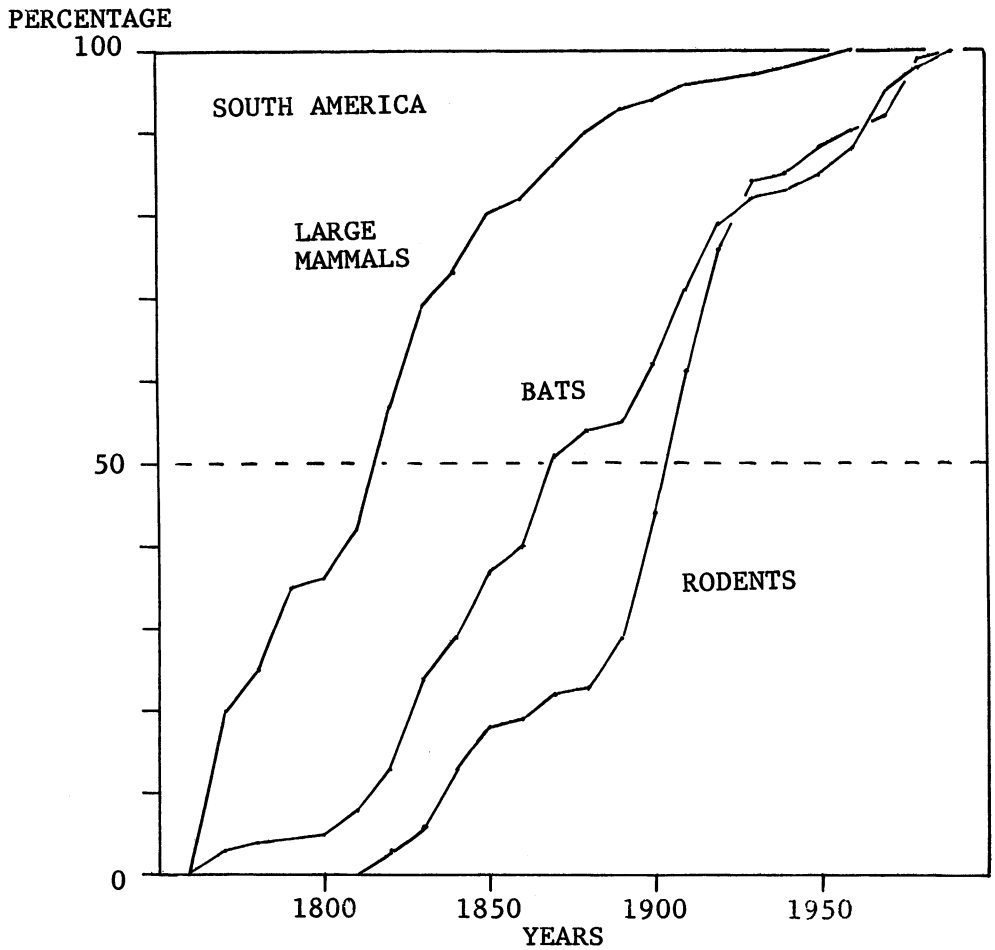

Fig. 2. Graph of cumulative numbers by decades of original descriptions of currently recognized South American species of large mammals, bats, and murid rodents.

within the separate continents approximately triples the mean range for North American species of bats but adds only 12% to the mean for South American bats.

Discovery curves such as those shown here for South American mammals (and in Steyskal, 1965, for other groups) tend to be sigmoid. Mammals and birds are comparatively well known and hence far along the curve for species, but neither of these groups has completely leveled. Most groups of animals (most of which are insects) are still on the first half of the curve, with little or no suggestion of leveling.

In summary, a major biological factor influencing time of discovery of a species is postulated to be range size. Predicted values for the geometric means for range sizes of South American rodents and large mammals are 3 and 20 ($\times 10^5$ km^2), respectively.

NEW RECORDS OF BOLIVIAN BATS

Since the publication of an annotated list of 79 species of bats known from Bolivia by Anderson et al. (1982), the following additional species have been reported. Anderson and Webster (1983) reported *Thyroptera tricolor tricolor* and *Vampyressa bidens.* Ibañez (1985) reported *Histiotus montanus* and *Molossops abrasus.* A specimen reported by Sanborn (1932) as *Molossops brachymeles,* a synonym of *M. abrasus,* has been reidentified as *Molossus molossus.* Torres et al. (1988) reported *Thyroptera discifera discifera* from the Beni. Ibañez and Ochoa (1989) reported *Pteronotus gymnonotus, Pteronotus parnelli, Pteronotus personatus, Nyctinomops aurispinosus, Nyctinomops macrotis, Eumops hansae, Promops centralis,* and *Promops nasutus.* The three species of the family Mormoopidae (all of the genus *Pteronotus*) are species that had been suspected to occur in Bolivia and are the first specimens of the family to be discovered there. They were obtained near the Serrania Huanchaca in northern Santa Cruz. Wilson and Salazar (1990) recently have discovered *Tonatia brasiliense* and *Vampyrops brachycephalus* in the Beni (most of the citations of "Anderson, 1985" in that paper should have been "Anderson, *in litt.*").

Below I report six species and one subspecies that have been discovered for the first time in Bolivia, along with some additional data on other recently reported species. Thus, 100 species are now known to occur in Bolivia.

Tonatia bidens (Spix, 1823): Dr. Masashi Harada (Laboratory of Experimental Animals, Osaka City University Medical School, Osaka 545, Japan, personal commun.) obtained a specimen in September 1984 at Chivé (12°23′S, 68°35′W; 180 m), in the department of Pando, identified as this species. I have not seen the specimen.

Vampyrum spectrum (Linnaeus, 1758): One specimen (American Museum of Natural History, AMNH 261379) was captured on 17 August 1985 in a mist net on the bank of the Río Tijamuchi (14°56′S, 65°09′W; 240 m), in the department of Beni. Measurements (in millimeters, except weight) are total length 161, no tail, hind foot with claws 30, ear from notch 49, weight 200 g, greatest length of skull 50.8, and condylobasal length of skull 43.3.

Vampyressa bidens (Dobson, 1878): Additional specimens (Museum of Southwestern Biology, MSB 57288; AMNH 261625–261627, 261633, 261640) have been obtained at Santa Ana de Madidi (12°34′S, 67°10′W; 240 m), in the department of La Paz, in September 1985 and August 1986; and (AMNH 262517) on the right bank of the Río Madre de Dios (11°26′S, 67°34′W; 160 m), also in La Paz, on 5 August 1986. Measurements are total length 54–62, forearm 34–39, and condylobasal length of skull 17.6–18.1. The middle upper incisors are slender and bifid, thus resembling those of *Uroderma,* and a median dorsal white stripe is present. The presence of only one pair of lower incisors differs from the two pairs present in *Uroderma.* The first specimen was reported by Anderson and Webster (1983).

Vampyressa pusilla thyone Thomas, 1909: Two specimens (AMNH 262524, 262559) were captured at Independencia (11°26′S, 67°34′W; 180 m) on 27 July and 7 August 1986, in the department of Pando. Measurements are total length 53, 50; forearm 32, 31.5; greatest length of skull 18.4, 17.8; and condylobasal length of skull 16.3, 15.6.

Diphylla ecaudata Spix, 1823: One speci-

men (AMNH 261777; MSB NK 13627) was captured on 16 September 1985 in a mist net near buildings of the Estancia Santa Ana de Madidi, in the department of La Paz. Measurements are total length 88, no tail, hind foot 18, ear from notch 18, weight 34 g, forearm 57, and condylobasal length of skull 20.1. The bat was a female with one embryo (26 mm crown–rump length).

Myotis riparius Handley, 1960: One specimen (AMNH 260251) was captured at the Estancia Cachuela Esperanza (16°47′S, 63°14′W; 300 m), in the department of Santa Cruz, on 22 August 1984.

Eptesicus brasiliensis andinus Allen, 1914: One specimen (AMNH 260257; MSB NK 12132) was captured on 13 September 1984 in a mist net in an arid area 5 km by road SE of Comarapa (17°58′S, 64°29′W; 1695 m), in the department of Santa Cruz. Measurements are total length 50, tail 13, hind foot 14, ear —, weight 10 g, forearm 48, greatest length of skull 18.4, and condylobasal length of skull 17.1.

Promops centralis Thomas, 1915: In addition to the three specimens reported by Ibañez and Ochoa (1989), three specimens (AMNH 260273, 260274; MSB 55188) were captured 4 through 8 October 1984 at Roboré (18°20′S, 59°45′W; 300 m), in the department of Santa Cruz. The highly vaulted palate is distinctive of *Promops*. Measurements are total length 135, 125, 137; tail 56, 46, 56; hind foot 11, 12, 12; ear 17, 17, 15; weight 21, 17, 20 g; forearm 52, 51, 53; greatest length of skull 20.4, 20.5, —; and condylobasal length of skull 18.6, 18.8, —.

Promops nasutus (Spix, 1823): In addition to a specimen reported by Ibañez and Ochoa (1989), two other specimens have been obtained in the department of Santa Cruz. One (AMNH 260306) was captured on 10 September 1984, 3 km by road SE of Comarapa (17°57′S, 64°30′W), and another specimen (AMNH 261851) was captured on 18 August 1985, 4.5 km N and 1.5 km E of Cerro Amboró on the Río Pitasama (17°45′S, 63°40′W; 620 m). Measurements are total length 105, 126; tail 33?, 50; hind foot —, 11; ear 14, 15; weight 16, 15 g; forearm —, 48; greatest length of skull 18.3, 19.2; and condylobasal length of skull 16.3, 17.4.

Nyctinomops laticaudatus laticaudatus (E. Geoffroy, 1805): Smaller bats of the subspecies *N. l. europs* Allen, 1899, have been previously known from the departments of Beni and La Paz. Measurements of the forearm for comparison with those below (minimum–maximum, N = 14, specimens from Magdalena in Beni at AMNH) are 41–44. The following 14 larger individuals from farther south can be referred to *N. l. laticaudatus*: AMNH 260265–260272 and MSB 55199–55203, captured 4–8 October 1984 at Roboré (18°20′S, 59°45′W; 300 m), in the department of Santa Cruz; AMNH 246653, captured 8 km S and 10 km E of Villa Montes (21°19′S, 63°25′W; 300 m), in the department of Tarija. Measurements (minimum–maximum, N = 14) are total length 103–116, head and body length 62–69, tail 37–47, hind foot 9–11, ear 17–22, weight 11–17 g, and forearm 45–49. Another specimen referable to *N. l. europs* (AMNH 262648; MSB NK 13967) was captured on 31 July 1986 in a mist net on the Isla Gargantua (12°23′S, 68°35′W; 180 m), in the department of Pando. Measurements are total length 99, tail 39, hind foot 11, ear 14, weight 9 g, forearm 43, and length of skull 17.0.

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An Analysis of Patterns of Distribution and Species Richness Among Philippine Fruit Bats (Pteropodidae)

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ABSTRACT

Twenty-three species of fruit bats (Pteropodidae) are known to occur in the Philippines. Fourteen of these (61%) are endemic to the archipelago. Patterns of distribution generally parallel the patterns exhibited by nonvolant mammals, indicating that the bats are influenced by similar historical phenomena. The maximum number of species known from a single Philippine island is 17, with up to 21 percent of the species on a single island being endemic. Distributions of seven species are limited to areas that comprised single islands during the late Pleistocene period of low sea level. Species richness within the Philippines is significantly correlated with island area; in comparison with nonvolant mammals, the slope of the species/area curve is low, and there is little variation related to isolation of the given island, implying that successful colonization by fruit bats is more frequent than among nonvolant mammals, although such colonization does not overwhelm other historical factors. This hypothesis of moderate levels of colonization is consistent with the presence of fruit bats on Krakatau and other recent volcanic islands, and with the presence in Indo-Australia of several very widespread species. Evidence from elsewhere in Indo-Australia indicates that aridity, extreme recency of origin, and isolation may reduce species richness on a given island. Analysis of preliminary phylogenetic data indicates that species of fruit bats have reached the Philippines from both the Sunda Shelf of Southeast Asia and from Sulawesi/New Guinea, and that several of the endemic species are members of a single phylogenetic clade that has undergone substantial diversification within the Philippines. There is little evidence of geological vicariance events in the Philippines, but Pleistocene sea-level vicariance events were common; however, there is little evidence of speciation dependent upon such processes. Biogeographic patterns and processes affecting fruit bats are fundamentally the same as those of nonvolant mammals, but the two groups differ in the rates of each process and so differ in the manner in which patterns are expressed.

INTRODUCTION

The origin and maintenance of patterns of biological diversity have been of central concern to evolutionary biologists since the days of Darwin and Wallace, and indeed their observations of these patterns were among the factors that led them to develop their theories of evolution. In spite of this long-standing interest, surprisingly few taxa have well-documented patterns of distribution and species richness, and in still fewer cases is there more than a superficial analysis of the causal origins of the patterns. The purpose of this paper is to present a preliminary analysis of the evolutionary and ecological processes that influence the patterns of diversity of one group of mammals, fruit bats of the family Pteropodidae, centered on one portion of their range, the Philippine Islands. In the course of this analysis, I present a series of testable hypotheses about patterns and processes that appear to exist within the Philippine bat fauna. This is done in part as a means of providing direction for future research efforts on these animals.

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Previous studies of Philippine mammals have focused primarily on nonvolant species (Heaney, 1986; Heaney et al., 1989; Heaney and Rickart, 1990; Rickart et al., 1991; and references therein), and these studies provide both a point of comparison and a series of questions and predictions regarding fruit bats. The comparison of fruit bats to nonflying mammals is productive because it allows testing of the general hypothesis that the biogeographic patterns exhibited by bats are fundamentally the same as those of nonvolant mammals because of the impact of common historical processes, in spite of the apparently greater vagility of bats. In this paper, I compare the biogeographic patterns of fruit bats on a point-by-point basis with those of nonvolant mammals in the Philippines in order to determine the degree and manner in which the two groups differ. Fruit bats are an appropriate group for such a comparison because they are relatively diverse (23 species in the Philippines), they are known to be strong fliers, they are relatively easily captured and inventoried (Heaney et al., 1989; Heideman and Heaney, 1989), and because they have been intensively studied by myself and my coworkers in the Philippines.

Previous studies of bats in large, well-known tropical archipelagos are limited to the Caribbean islands (Koopman, 1975, 1989a; Morgan and Woods, 1986; Griffiths and Klingener, 1988; Phillips et al., 1989) and the Bismarck and Solomon Islands to the east of New Guinea (Phillips, 1968; Koopman, 1979, 1982; Smith and Hood, 1981). Authors of these studies have provided evidence that colonization, extinction, and speciation (including vicariance processes) each have played significant roles in determining patterns of species richness and distribution. Analyses by these authors generally have found evidence that colonization rates are high, although only Morgan and Woods (1986) provided a numerical estimate; that was of one successful colonization per half-million years, about three times the rate of nonvolant mammals in the same area. Extinction was considered in detail only by Morgan and Woods (1986), who were able to use a superb fossil record to document an extinction rate of one event per 2500 years during the last 20,000 years; several other authors gave no consideration to the impact of extinction. Speciation is generally acknowledged by these authors to be a significant generative force; most believe it to result from colonization events, but others present evidence for the role of geological vicariance events (Smith and Hood, 1981; Griffiths and Klingener, 1988).

In this paper I focus primarily on comparison of faunas, rather than on documentation of distribution of individual species as has Koopman (1989b). In order to make quantitative comparison of these faunas meaningful, I focus on those islands whose fruit bat faunas have been thoroughly inventoried; these include 7 Philippine islands and 13 additional islands from adjacent portions of Indo-Australia. Because so few attempts have been made to measure rates of the processes that influence species richness and distribution, even roughly (Heaney, 1986; papers cited above), one purpose of this paper is to estimate rates of these processes for fruit bats.

Geology of the Study Area

All currently available evidence indicates that the modern Philippine archipelago (Figs. 1, 2) originated de novo from the ocean floor (see reviews by Hamilton, 1979; Hashimoto, 1981; Fuller et al., 1983; Heaney, 1986; Mitchell et al., 1986; Defant et al., 1989). Some of the geological processes that formed the modern Philippines originated on the continent by rifting of a small amount of continental material eastward into the Pacific (Holloway, 1982; Taylor and Hayes, 1983; Mitchell et al., 1986). However, the fragmentary remnants of this portion of the modern Philippines (in parts of Palawan, Mindoro, and Panay) are capped by thick marine sediments, and current evidence indicates that those fragments were below sea level for several million years. All the current islands are composed of material that has been thrust above sea level by tectonic and volcanic activity associated with the many subduction zones that bracket the archipelago. Most of the growth of the islands has occurred since the beginning of the Miocene, and much since the Pliocene, with most current topology probably close to its maximum level.

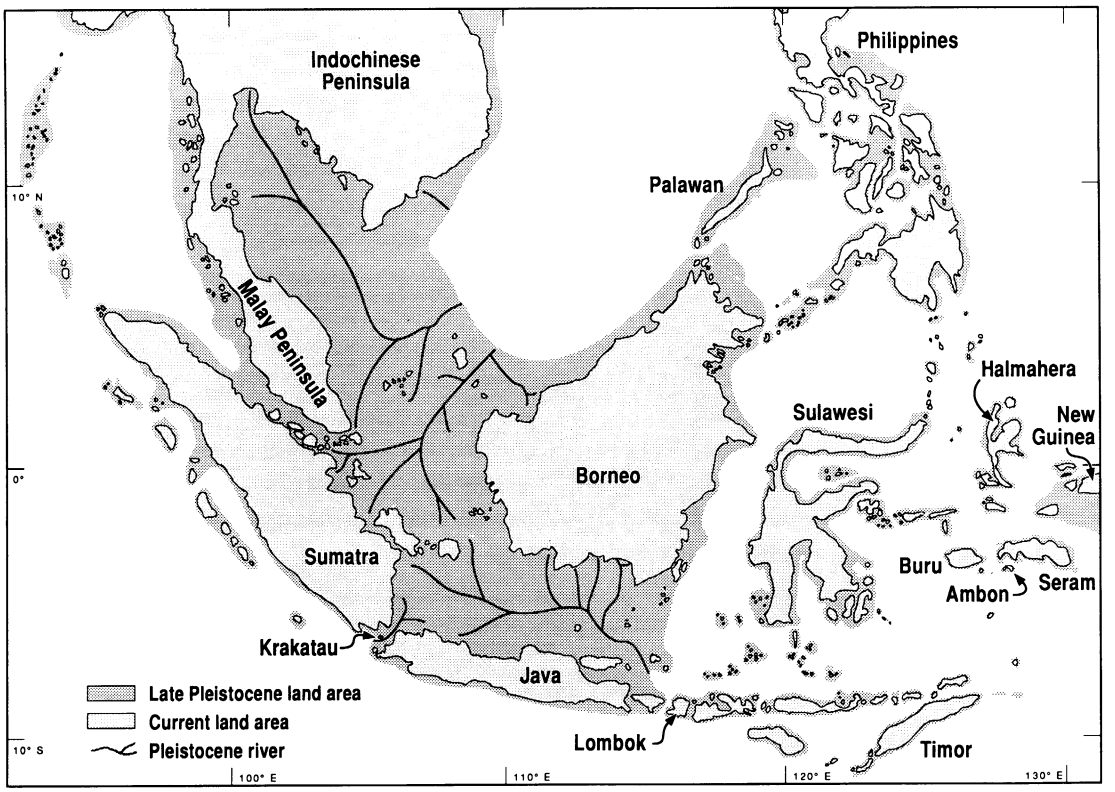

Fig. 1. Map of Southeast Asia and adjacent portions of Indo-Australia, showing the locations of current and Pleistocene islands discussed in the text. Late Pleistocene land limits were based on the 120-m bathymetric line, and the locations of rivers were plotted from topographic features (see Methods).

Because the islands are on a shallow platform, they were heavily influenced by repeated Pleistocene changes in sea level. A map of the likely configuration of the islands during the late Pleistocene, at which time the land area was at or close to its maximum extent, is presented in figure 2. Current islands were combined into a smaller number of larger islands, with most merging into only four islands: Greater Luzon, Greater Mindanao, Greater Palawan, and Greater Negros-Panay. These large Pleistocene islands are synonymous with faunal regions that have been described elsewhere (Heaney, 1986). The present configuration of the islands represents a phase of fragmentation due to high water levels.

One portion of the archipelago, the Palawan chain, was joined to the Asian mainland during the middle Pleistocene period of low sea level, when sea level dropped to about 160 m below the present level (references in Heaney, 1986). The San Bernardino Channel between Greater Mindanao and Luzon might also have been dry at this time, although late Pleistocene volcanic activity (centered at Mt. Bulusan) raised the level of southern Luzon during the late Pleistocene.

Geological fragmentation of landmasses probably has occurred within the archipelago, but details are scanty. The Philippine fault, which runs through the archipelago from western Luzon (at the head of Lingayan Gulf) to the northernmost tip of Mindanao, has certainly been associated with splitting of the "Philippine shelf" by the deep channels that separate the landmasses of Greater Luzon, Greater Mindanao, and Greater Negros-Panay, as shown in figure 2. However, it seems certain that at least some and perhaps all of the fragmentation of these three landmasses took place beneath shallow seas; in other

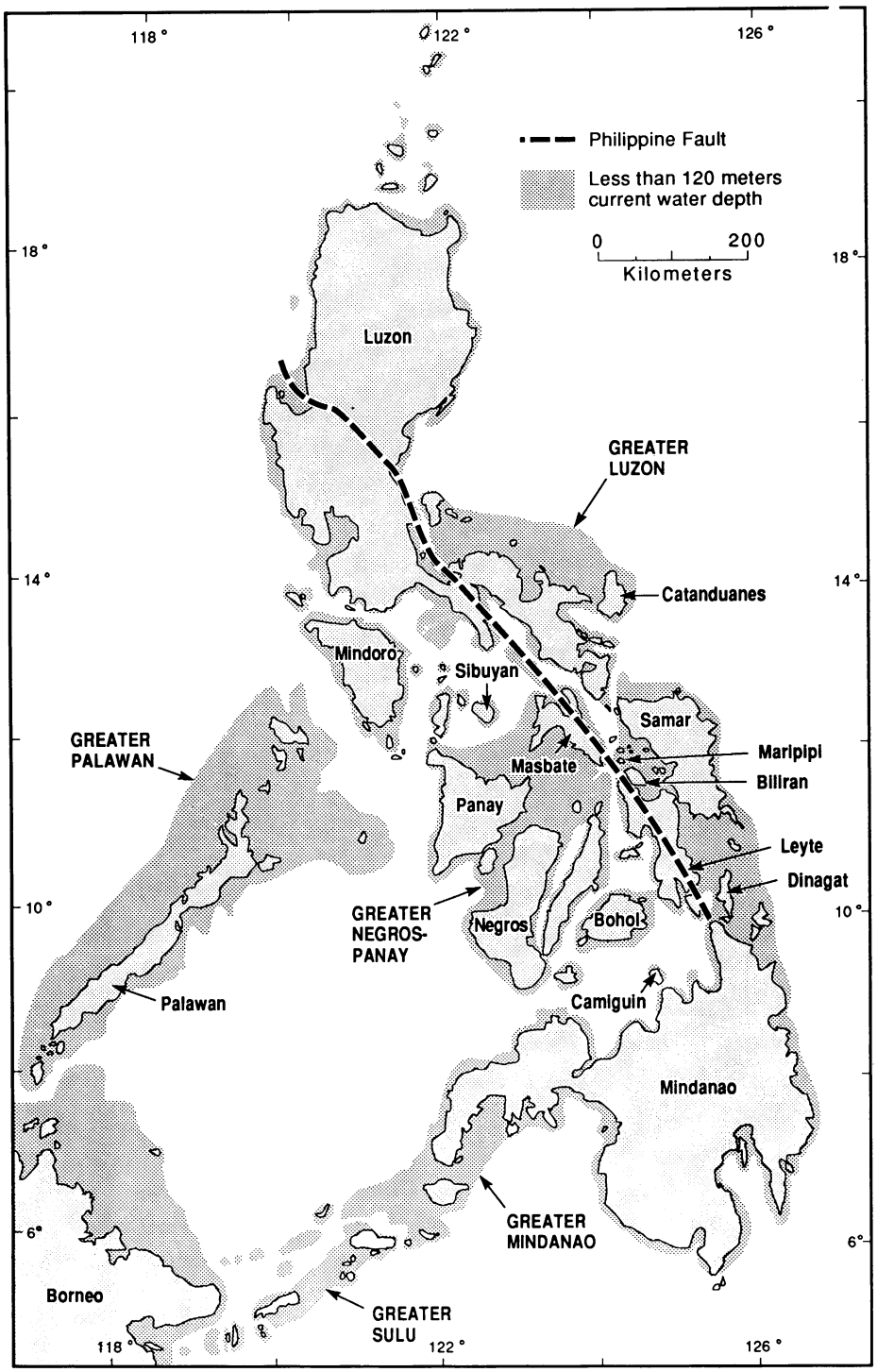

Fig. 2. Map of the Philippine Islands, showing the locations of current and Pleistocene islands (from Heaney, 1986).

words, the islands may not have been connected as a dry landmass (Hashimoto, 1981; Defant et al., 1989). In this analysis, both possibilities (i.e., fragmentation pre- and postemergence from subaqueous conditions) are considered, but it seems most likely that most of the effects of any such fragmentation have been overwhelmed by the influence of rising land levels and by Pleistocene changes in sea level.

The available geological evidence thus indicates that the main body of the Philippines, excluding the Palawan chain, has arisen de novo from the ocean floor and has had no connection to the Asian mainland above water. In this context, it is useful to distinguish between two types of oceanic (non-landbridge) islands. The first includes the large, old islands of Greater Luzon and Greater Mindanao, both of which had large land areas by the Miocene. The second includes the smaller, often volcanically active islands that have originated more recently and are isolated from the older islands by deep channels. Important members of the latter group are Mindoro, which originated in the Mio-Pliocene (ca. 8–10 million years before present [Ma BP]); Negros (joined with Panay and Cebu as a larger island during the Pleistocene), probably no older than ca. 1–4 Ma BP (Schwab, 1982); and Camiguin and Sibuyan, both active volcanic cones of Pleistocene age (ca. 0.10–1 Ma BP).

Methods

Specimens examined for this study are housed in the American Museum of Natural History, Delaware Museum of Natural History, Field Museum of Natural History, University of Michigan Museum of Zoology, and U.S. National Museum of Natural History. Previously unpublished records of Philippine fruit bats are available upon request; all records are in the process of being described in detail.

The limits of land in the map of Pleistocene Southeast Asia (fig. 1) were determined in the same fashion as in figure 2 (from Heaney, 1986), that is, by tracing the current 120-m bathymetric line around all areas above that level, using detailed bathymetric maps published by the U.S. Defense Mapping Agency (scale 1:500,000 to 1:50,000). The locations of major Pleistocene rivers was determined by tracing topographic features on the same maps; in nearly all cases, the configuration of a river channel was clearly apparent. The course of rivers is shown only where the course was unambiguous; ambiguity was often encountered near the mouths of modern rivers, where modern sediments obscure the ancient channels. I made no attempt to compensate for modern sea-floor tidal scouring or recent tectonic changes.

Cluster analyses were run on an AT&T 6386 microcomputer using a Basic program written by R. E. Strauss. The clustering algorithm was the unweighted pair-group method (UPGMA); standard errors were calculated by iterative removal of each member of a given cluster, and defined as the standard deviation of distances divided by the number of distances. Regression analysis and 95% confidence limits were calculated on the same computer using SAS version 6.03 (SAS Institute, Inc., 1988), using the least-squares method.

For convenience, I include peninsular Malaysia in analyses and discussion as if it were an island. It is not, of course, because there is continuous land to the Asian mainland. It thus serves as a mainland reference point. However, it is somewhat isolated, and is unlike Indochina and adjacent areas on the continent in supporting a fauna that is characteristic of the large islands on the Sunda Shelf, with the faunal boundary located approximately at the Isthmus of Kra (Boonsong and McNeely, 1977).

This analysis includes only the 20 islands with the most intensively surveyed fruit bat faunas in Indo-Australia. It is likely that at least a few additional species actually exist on these islands but have not been documented, and their discovery will change the picture presented here. However, I point out that it is impossible ever to know when all species have been found, and I believe that it is best to move ahead with the best data available, with the realization that all research produces only an approximation of reality, to be refined and extended by future researchers. I emphasize that finding those last species, and adding more islands to the list, is highly desirable.

The depiction of fruit bat phylogeny used in this paper is derived from the classic study of Andersen (1912), redrawn by Heaney and Rickart (1990) using current conventions to show Andersen's conclusions, and placing recently described genera using Andersen's character sets. It is the only comprehensive analysis of the group that is currently available. Although the study is old, Andersen was remarkably thorough and modern in his approach, especially in defining characters precisely, in defining and considering polarity of those characters, and in explicitly defining phylogenetic hypotheses in diagrams of branching sequences. However, he did use some shared primitive characters in defining some nodes, he placed some taxa basally rather than on terminal branches, and he considered patristic distance in his final classification, and these limitations should be borne in mind by the reader. Future studies are likely to differ from some of his conclusions, but his hypotheses form a useful and irreplaceable component for current studies.

Acknowledgments

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RESULTS AND DISCUSSION

Species Richness and Island Area: The number of fruit bat species known from a single Philippine island varies from 10 to 17 (this includes only those islands that have been intensively surveyed; tables 1–3). A regression of number of species on island area is highly significant (fig. 3; table 4; $r = 0.92$). Several other islands in Indo-Australia appear to fall on the same regression line (Borneo [point 1 in fig. 3], Sumatra [2], Peninsular Malaysia [3], and New Guinea [20]), implying a commonality of processes over a wide region, although no small islands outside of the Philippines have been intensively surveyed. The homogeneity in species richness implies a homogeneity of processes that influence species richness within this set of islands.

A comparison with other islands in nearby Indo-Australia shows the existence of substantially greater variation. One of the 13 islands, Sulawesi, lies above the 95% confidence limits for the Philippines. Sulawesi (13) has the richest known pteropodid fauna, even though it is substantially smaller in area than three other islands (Borneo, Sumatra, and New Guinea). Sulawesi is unique in that it is the only large island that lies between the two continental source areas; perhaps its high species richness is due to its accessibility to colonizing species. Three islands fall significantly below the species/area curve for the Philippine fauna. Timor (14) is notably more arid than any other. Krakatau (5) is well below the expected value; it is an island near Java and Sumatra that exploded in 1883, destroying all vegetation and mammals, and

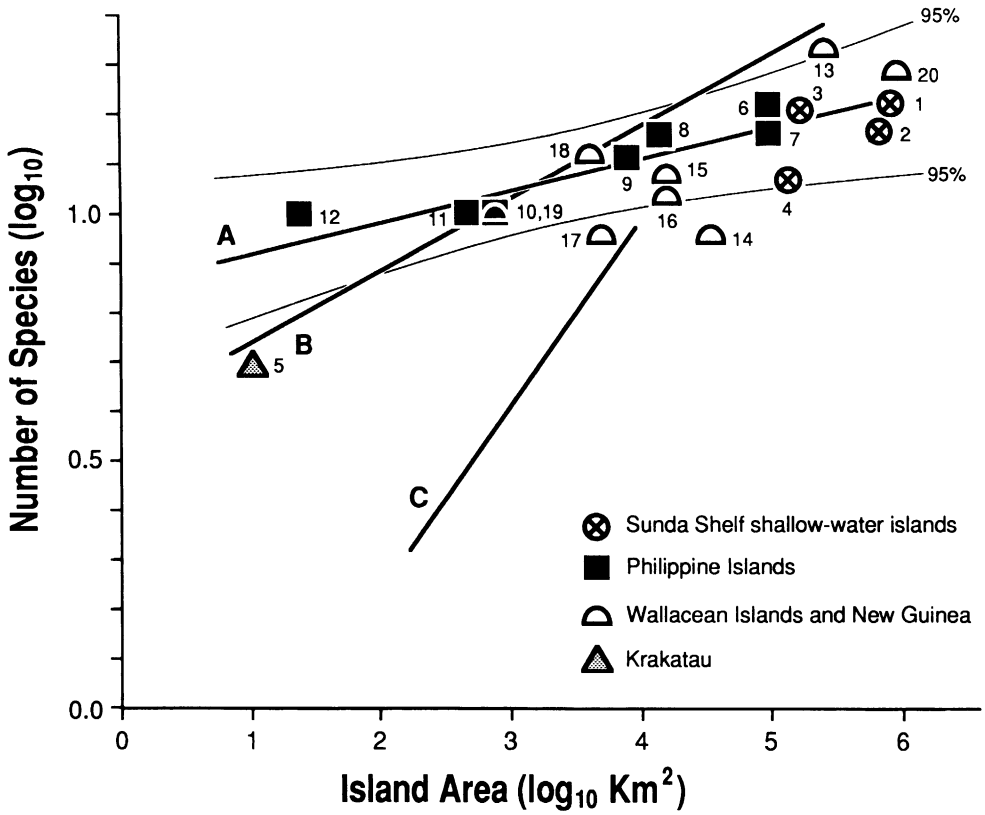

Fig. 3. Plot of the number of species of fruit bats against island area for 20 well-known islands in Indo-Australia. The numbers correspond to those in table 5. Regression line **A** is for Philippine fruit bat faunas only; the dotted lines indicate 95 percent confidence limits. Regression lines **B** and **C** are for nonvolant mammals on Luzon and Mindanao land-bridge islands and for Philippine isolated oceanic islands, respectively. Statistics for all lines are in table 4.

has subsequently been repopulated by over-water colonization. Buru (17) is also species-poor for its size; it is marked among this series for its isolation relative to larger, more species-rich source areas (fig. 1), especially in terms of its distance from large Pleistocene islands and major source areas. Halmahera (15) and Seram (16), which are also rather isolated, also tend to be species-poor, though not significantly so. On the basis of these data, I hypothesize that moderate aridity, extreme recency of origin, and/or substantial isolation of a given island will result in relatively low species richness of fruit bats.

ENDEMISM AND ISLAND AREA: On a given Philippine Pleistocene island, from 7% to 21% of the fruit bat species are endemic (table 3). The smallest single current islands that support endemic species are Panay and Negros (12,300 km^2 and 13,670 km^2, respectively). This is an order of magnitude smaller than the limit for the presence of endemics on the Sunda Shelf, where no endemic species are present on single current islands smaller than Java (125,630 km^2), but similar to other isolated oceanic islands in Wallacea such as Halmahera (17,790 km^2), which has one endemic species. Although the largest island (New Guinea) has the largest number of endemics (five), there is no correlation between the number of endemic fruit bat species and island area ($N = 8$, $r = 0.39$, $P > 0.05$) on those islands in table 5 known to support endemics.

PATTERNS OF GEOGRAPHIC DISTRIBUTION WITHIN ISLAND GROUPS: There are 23 species of fruit bats currently known from the Philippines (tables 1, 2; Heaney et al., 1987). Of

TABLE 1
Distribution of Fruit Bats on Seven Intensively Inventoried Islands in the Philippines

	Distribution type[a]	Island[b]						
		Luz	Neg	Mdn	Ley	Din	Bil	Mar
Acerodon jubatus	Phil	X	X	X	X	X	X	X
A. lucifer[c]	Neg	—	—	—	—	—	—	—
A. leucotis[d]	Pal	—	—	—	—	—	—	—
Alionycteris paucidentata	Mind	—	—	X	—	—	—	—
Cynopterus brachyotis	Wide	X	X	X	X	X	X	X
Dobsonia chapmani	Neg	—	X	—	—	—	—	—
Dyacopterus spadiceus	Near	X	—	X	—	—	—	—
Eonycteris robusta	Phil	X	X	X	X	—	X	X
E. spelaea	Wide	X	X	X	X	—	X	X
Haplonycteris fischeri	Phil	X	X	X	X	X	X	—
Harpyionycteris whiteheadi	Phil	X	X	X	X	—	X	X
Macroglossus minimus	Wide	X	X	X	X	X	X	X
Megaerops wetmorei	Near	—	—	X	—	—	—	—
Nyctimene rabori	Neg	—	X	—	—	—	—	—
Otopteropus cartilagonodus	Luz	X	—	—	—	—	—	—
Ptenochirus jagori	Phil	X	X	X	X	X	X	X
P. minor	Mind	—	—	X	X	X	X	—
Pteropus hypomelanus	Wide	X	X	X	X	X	—	X
P. leucopterus	L/M	X	—	—	—	X	—	—
P. pumilus	Phil	X	X	X	X	—	—	X
P. speciosus	Near	—	—	X	—	—	—	—
P. vampyrus	Wide	X	X	X	X	X	—	—
Rousettus amplexicaudatus	Wide	X	X	X	X	X	X	X
Total		15	14	17	13	10	10	10

[a] Phil, widespread in oceanic Philippines; Luz, restricted to Greater Luzon; Mind, restricted to Greater Mindanao; Neg, restricted to Greater Negros-Penay; Pal, restricted to Greater Palawan; L/M, Luz + Mind; Near, restricted to Philippines and nearby continental shelf island(s); Wide, widespread in Southeast Asia.

[b] Luz, Luzon; Neg, Negros; Mdn, Mindanao; Ley, Leyte; Din, Dinagat; Bil, Biliran; Mar, Maripipi. For locations, see figure 2.

[c] *Acerodon lucifer* has been taken only on Panay and is believed to be extinct (Heaney and Heideman, 1989).

[d] *Acerodon leucotis* is known only from Palawan, Balabac, and Busuanga (Musser et al., 1982).

the nine (39%) nonendemic species, six are widespread in Indo-Australia and three are shared with nearby islands on the continental shelf of Asia (table 2). The widespread species (table 1) generally occur from Indochina (and sometimes India) through the Greater Sunda Islands, the Philippines, and Sulawesi, sometimes extending to New Guinea and Australia. The three that occur on nearby islands are *Dyacopterus spadiceus* (on Borneo, Sumatra, and the Malay Peninsula), *Megaerops wetmorei* (on Mindanao and Borneo only), and *Pteropus speciosus* (on Mindanao and the Sulu Islands in the Philippines and on two small islands in the Java Sea).

Of the 14 endemic species (61% of the fau-

TABLE 2
Summary of Distribution Patterns of Philippine Fruit Bats (Pteropodidae)
(The extent of Pleistocene islands is defined in the text and figure 2)

Species in the Philippines (total)	23
Species widespread in Indo-Australia	6 (26%)
Species shared with nearby archipelagos	3 (13%)
Endemic species widespread in oceanic Philippines	6 (26%)
Endemic species on two or more Pleistocene islands	1 (4%)
Endemic species on only one Pleistocene island	7 (30%)

TABLE 3

Summary of Species Richness and Endemism of the Pteropodid Fauna of the Philippines

(Names of islands refer to Pleistocene islands, as defined in text and figure 2. Numbers in parentheses refer to islands that are incompletely surveyed.)

	No. indigenous species	No. endemic species	Percent endemic
Greater Luzon	15	1	7
Greater Mindanao	17	2	12
Greater Palawan	(7)	1	(14)
Greater Mindoro	(10)	0	(0)
Greater Negros-Panay	14	3	21
Greater Sulu	(7)	0	(0)

na; table 2), there are 6 (26%) that occur throughout the archipelago with the exception of the Palawan chain (table 1). One species occurs only on Luzon (*Otopteropus cartilagonodus*), two only on the islands that made up Greater Mindanao (*Alionycteris paucidentata* and *Ptenochirus minor*), one on Palawan and nearby small islands (*Acerodon leucotis*), and three on Greater Negros-Panay (*Acerodon lucifer, Dobsonia chapmani,* and *Nyctimene rabori*). One species (*Pteropus leucopterus*) occurs on Greater Luzon and on a small island (Dinagat) that was part of Greater Mindanao (Heaney and Rabor, 1982).

These data indicate that there are four underlying patterns of distribution of fruit bats that occur in the Philippines. First, about a quarter of the fruit bats (six species, or 26%) are shared by the Philippines and much of Southeast Asia. Members of a second group (composed of three species) occur in the Philippines (especially the southern islands) and on the islands of the Sunda Shelf, especially the adjacent island of Borneo. Third, about a quarter of the species (six, or 26%) are restricted to the oceanic portion of the Philippines (i.e., exclusive of the Palawan group). Finally, fruit bats in the largest group (eight species, or 35%) are restricted within the Philippines to one (or in one case, two) of the large islands that existed during Pleistocene periods of low sea level.

It should be noted that there are clear ecological differences between the widespread, nonendemic species and the endemic species: the former are rare or absent from primary forest but are typically abundant in disturbed habitats, whereas the latter are strongly associated with primary forest (Heideman and Heaney, 1989; Heaney and Rickart, 1990).

In contrast, although the fruit bat fauna on the islands of the continental shelf of Southeast Asia (the Sunda Shelf) is equally rich (21 species versus 23 in the Philippines), there is a greater degree of intraregional homogeneity (table 6; Appendix). Only six species (29%) are endemic to the Sunda Shelf (versus 61% in the Philippines), and only two (10%) are restricted to single islands (*Eonycteris major* and *Megaerops kusnotoi*), in comparison with five (22%) restricted to one of the current Philippine islands. I suggest that the relative homogeneity on the Sunda Shelf is due to the same historical factor as the homogeneity within the current islands of Greater Mindanao: both areas were exposed as continuous dry land during the late Pleistocene (fig.

TABLE 4

Regression Line Sample Sizes (N), Correlation Coefficients (*r*), Slopes, and Intercepts for Philippine Fruit Bats, Indigenous Nonvolant Mammals in the Luzon and Mindanao Groups, and Indigenous Nonvolant Mammals on Geologically Young, Isolated Philippine Islands

(Statistics for Philippine fruit bats from this paper, for nonvolants from Heaney [1986])

	N	Correlation coefficient (r)[a]	Slope	Intercept
Philippine fruit bats	7	0.92**	0.066	0.86
Luzon/Mindanao nonvolants	4	0.97*	0.17	0.61
Isolated nonvolants	3	0.92	0.44	−0.74

[a] *, significant at 0.05 level; **, significant at 0.01 level.

1; see also Heaney and Rabor, 1982; Whitmore, 1984; Heaney, 1986).

The fruit bat faunas of the Molucca Islands, Sulawesi, Timor, and New Guinea are quite different from those of the Philippines and the Sunda Shelf (Appendix). Only within the southern Moluccas are there enough intensively surveyed islands to make meaningful quantitative statements about local variation. The fruit bat faunas of Ambon, Buru, and Seram are extremely similar, with Ambon and Buru differing from Seram only in lacking one or two species (Appendix). There are no single-island endemics in the group, but 3 of the 11 species (27%) may be viewed as endemics of the Molucca Islands (*Pteropus chrysoproctus, P. melanopogon,* and *P. ocularis*). It should be noted that there is one single-island endemic in the northern Moluccas (*Syconycteris carolinae* from Halmahera [Rozendaal, 1984]), as well as a more general north Moluccan endemic (*Pteropus personatus*).

QUANTITATIVE SIMILARITIES BETWEEN ISLAND GROUPS: In order to quantify patterns of fruit bat faunal similarity within Indo-Australia, I calculated Simpson's Index of Similarity (Udvardy, 1969) for the 20 islands included in table 5. This is the index of choice when the numbers of species in the various samples differ substantially (in this case, from 5 to 21), and there are few ubiquitous (or nearly ubiquitous) taxa (in this case, only three: *Eonycteris spelaea, Macroglossus minimus,* and *Rousettus amplexicaudatus*). The faunal similarity indices (table 7) were then subjected to UPGMA cluster analysis, with an estimate made of the standard error associated with each node connecting three or more faunas (see Methods). I have avoided interpreting some clustering sequences when the standard errors indicate that those patterns were not statistically meaningful.

The results (fig. 4) indicate the presence of four major faunal groupings. The first of these is composed of bats from islands on the Sunda Shelf of Southeast Asia, with Sumatra, Krakatau, and Java forming a subgroup distinct from the Malay Peninsula and Borneo; the Lesser Sunda islands of Lombok and Timor form a distinctive adjunct to this group. The second group consists of bat faunas on islands in the Philippines, with no interpretable pattern within the group except for the similarity of Mindanao, Leyte, and Biliran. The third group consists of Sulawesi and the southern Moluccas (Ambon, Buru, and Seram). Finally, the fourth group consists of Halmahera and New Guinea. Sulawesi and the southern Moluccas link with Halmahera and New Guinea, and the Philippines with the Sunda Shelf and Lesser Sunda islands, at the highest levels.

TABLE 5

Area and Number of Species of Fruit Bats Occurring on 20 Selected Islands in Indo-Australia, by Region

(Data from tables 1 and 6 and Appendix)

	Area (km^2)	Number of species	Number of endemic species
Sunda Shelf			
1. Borneo	743,244	17	1
2. Sumatra	473,607	15	0
3. Peninsular Malaysia	131,676	16	0
4. Java	125,628	12	1
5. Krakatau (Rakata)	12	5	0
Philippines			
6. Mindanao	99,078	17	1
7. Luzon	108,171	15	1
8. Negros	13,670	14	2
9. Leyte	7213	13	0
10. Dinagat	670	10	0
11. Biliran	498	10	0
12. Maripipi	22	10	0
Wallacea			
13. Sulawesi	189,035	21	3
14. Timor	35,480	9	0
15. Halmahera	17,790	12	1
16. Seram	16,720	11	0
17. Buru	8786	9	0
18. Lombok	4729	13	0
19. Ambon	597	10	0
Australian continental shelf			
20. New Guinea	854,700	20	5

PHYLOGENETIC RELATIONSHIPS: The geographic origin of the Philippine fruit bat fauna can be assessed in two ways. The first and more crude of the two is to determine the geographic location of the sister-species of the taxa in the Philippines, or, when that is not

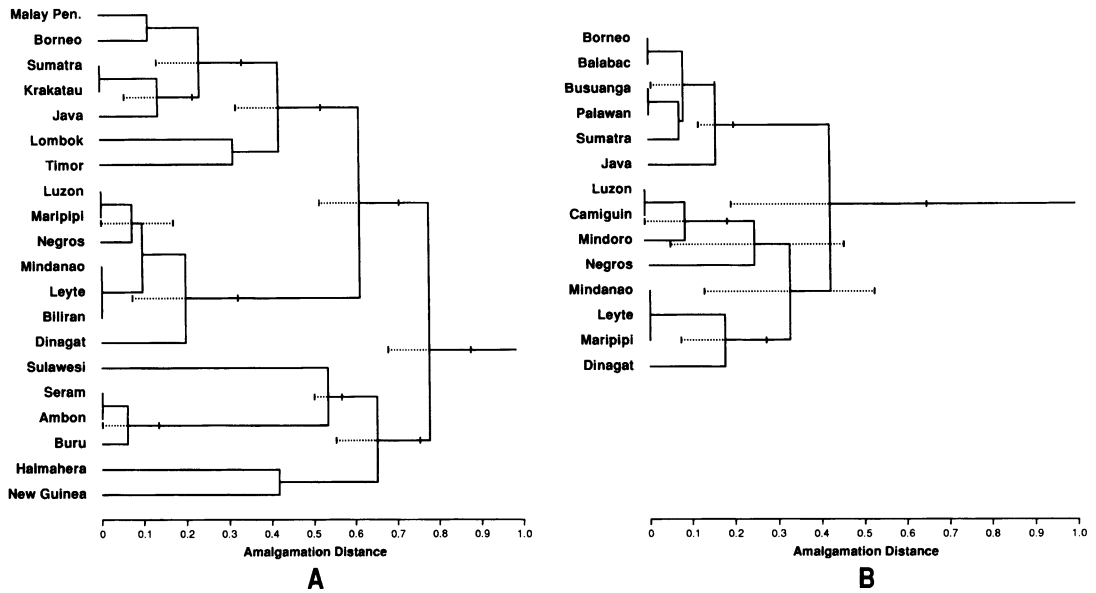

Fig. 4. Results of a cluster analysis of fruit bat faunal similarity indices (**A**) for 20 well-known islands in Indo-Australia, using Simpson's index of similarity, and for nonvolant mammal faunas (**B**) on a subset of these. Data for A from table 7, B from Heaney (1986). Interrupted bars show standard errors for the nodes (see Methods).

known, the location of other congeners. This approach is usable only for those genera that are not endemic to the Philippines; it is the same methodology used for nonvolant mammals by Heaney (1986). Data concerning the species for which geographic sister-species are known are summarized in table 8. Four genera are widespread in Indo-Australia, and so might have entered the Philippines from any area to the south. Five species have their closest relatives on Sulawesi, and three on Borneo. There is no evidence that any species entered the Philippines from the north, where the fruit bat fauna is depauperate (Tate, 1946; Koopman, 1989a).

The second approach involves use of phylogenetic relationships on a finer scale. The current working hypothesis of phylogenetic relationships among the majority of Indo-Australian fruit bat genera is shown in figure 5; the remainder (*Eonycteris, Macroglossus,* and *Syconycteris*) form part of an outgroup to those depicted, and the *Pteropus* branch includes *Acerodon, Neopteryx,* and *Styloctenium* (Miller, 1907; Andersen, 1912; Rickart et al., 1989). The nonendemic Philippine genera are members of at least five different major clades. I interpret this pattern as indicating that each of the five arrived in the Philippines independently. Further, although *Dobsonia* and *Harpyionycteris* are shown here as a monophyletic group, they are quite different morphologically and are often considered to be more distantly related (e.g., Miller, 1907), and each has an identifiable sister species on Sulawesi (table 8). I therefore count each of these as having reached the Philippines independently.

Eight of the 14 endemic Philippine fruit bat species are members of a monophyletic clade (labeled "Cynopterus group"); in other words, a majority of the endemic Philippine fruit bat species are very closely related. Further, the four most derived genera in this clade (with five species) are entirely confined to the Philippines; this implies that their evolution has occurred solely within the Philippines. In other words, 22% (5 of 23 species) of the current species richness is due to speciation within the Philippines. Four of the five species in this clade occur sympatrically on Mindanao. Of the six remaining endemic

species, two are members of a genus (*Acerodon*) confined to Wallacea (the islands between the continental shelves of Asia and Australia), two are members of genera that are most diverse in the New Guinea region (*Dobsonia* and *Nyctimene*), and two are members of a genus widespread in Indo-Australia (*Pteropus*; for further discussion, see Musser, 1987; Koopman, 1989b).

Taken together, these data indicate that the current fruit bat fauna of the oceanic portion of the Philippines has resulted from about 12 independent colonization events.

THE ROLE OF VICARIANCE EVENTS: There are three points within the oceanic Philippines where geological vicariance events might have taken place; these are at the San Bernardino Strait, between Luzon and Samar (a part of Greater Mindanao); at the Verde Island Passage between Luzon and Mindoro; and at the Masbate Passage between Masbate and both Luzon and Samar (fig. 2). If geological splitting of a formerly contiguous landmass had occurred between any of these areas associated with the Philippine Fault, then one might expect to see sister taxa distributed on these areas; acceptable evidence of a geological/phylogenetic pattern in such cases is dependent on repetition among several lineages (Humphries and Parenti, 1986; Cracraft, 1988).

Biological evidence of vicariance events within the Philippines is slight and ambiguous. There are no pairs of congeneric species that have the predicted relationship. However, there is one sister-genus relationship that conforms to one of the expected patterns: *Alionycteris,* a monotypic genus restricted to Mindanao, and *Otopteropus,* a monotypic genus restricted to Luzon, form a monophyletic group (fig. 5). This might represent the result of a vicariance event, but a single observation does not establish the existence of a general pattern. No other sister-taxon relationships within these bats are evident that conform to these potential geological patterns.

There are two additional points where geological vicariance events might have taken place. The first is along the Sangihe Arc between Sulawesi and Mindanao. There are four sister-species pairs in these two areas that form a consistent pattern: *Dobsonia exoleta/D. chapmani, Harpyionycteris celebensis/H. whiteheadi, Nyctimene cephalotes/N. rabori,* and *Pteropus griseus/P. speciosus* (table 8). The Philippine species (listed second in each of these pairs) is believed to be the more derived species in each case. Thus, there is evidence of a consistent pattern. However, two objections may be raised to a vicariance interpretation. First, the Sangihe Arc is currently an irregular feature, with several channels over 1000 m deep, and there is no evidence that it has ever been either more complete or appreciably higher (Hamilton, 1979: 191; Moore and Silver, 1983). Second, the pattern predicted by the vicariance model is, in this case, identical to the one predicted by the equilibrium model, given the latter's emphasis on dispersal from one species-rich source (Sulawesi) to less species-rich, more isolated islands (the Philippines). Thus, it is not possible to discriminate between the

TABLE 6

Fruit Bats Recorded on Borneo, Sumatra, Peninsular Malaysia, and Java

(Species endemic to the Sunda Shelf are indicated by asterisks. Data from Hill [1983] and Payne et al. [1985].)

	Borneo	Sumatra	Malay Pen.	Java
Aethalops alecto	X	X	X	X
*Balionycteris maculata**	X	–	X	–
Chironax melanocephalus	X	X	X	X
Cynopterus brachyotis	X	X	X	X
*C. horsfieldi**	X	X	X	X
C. sphinx	X	X	X	–
C. titthaecheileus	–	X	–	X
Dyacopterus spadiceus	X	X	X	–
*Eonycteris major**	X	–	–	–
E. spelaea	X	X	X	X
Macroglossus minimus	X	X	X	X
M. sobrinus	–	X	X	X
Megaerops ecaudatus	X	X	X	–
*M. kuznotoi**	–	–	–	X
M. wetmorei	X	–	–	–
*Penthetor lucasii**	X	–	X	–
Pteropus hypomelanus	X	–	X	–
P. vampyrus	X	X	X	X
Rousettus amplexicaudatus	X	X	X	X
R. leschenaultii	–	X	X	X
*R. spinalatus**	X	X	–	–
Total	17	15	16	12

TABLE 7

Simpson's Similarity Indices for the Fruit Bat Faunas of 20 Selected Islands in Indo-Australia

(Compiled from data in tables 1 and 6 and Appendix)

	Luz	Neg	Min	Ley	Din	Bil	Mar	Bor	Sum	Mal	Jav	Hal	Kra	Ngu	Sul	Tim	Ser	Amb	Bur	Lom
Luzon	—	.86	.87	.92	.90	.90	.99	.47	.40	.47	.42	.25	.20	.20	.33	.44	.18	.20	.11	.38
Negros		—	.86	.92	.80	.90	.99	.43	.36	.43	.38	.25	.20	.21	.36	.44	.18	.20	.11	.38
Mindanao			—	.99	.90	.99	.99	.47	.40	.44	.42	.25	.20	.18	.29	.44	.18	.20	.11	.38
Leyte				—	.90	.99	.99	.46	.38	.46	.42	.25	.20	.23	.38	.44	.18	.20	.11	.38
Dinagat					—	.70	.60	.50	.40	.50	.40	.30	.20	.30	.40	.33	.20	.20	.11	.40
Biliran						—	.80	.40	.40	.40	.40	.20	.20	.20	.40	.33	.20	.20	.11	.40
Maripipi							—	.50	.40	.50	.40	.30	.20	.30	.50	.44	.20	.20	.11	.40
Borneo								—	.80	.88	.67	.25	.60	.18	.35	.44	.18	.20	.11	.62
Sumatra									—	.87	.92	.17	.99	.13	.33	.55	.18	.20	.11	.69
Malay Peninsula										—	.83	.25	.80	.19	.38	.44	.18	.20	.11	.62
Java											—	.17	.80	.17	.42	.55	.18	.20	.11	.69
Halmahera												—	.20	.58	.42	.22	.27	.30	.22	.17
Krakatau													—	.20	.20	.40	.20	.20	.20	.60
New Guinea														—	.30	.33	.45	.50	.33	.31
Sulawesi															—	.56	.45	.50	.44	.38
Timor																—	.33	.33	.22	.67
Seram																	—	.99	.99	.18
Ambon																		—	.89	.20
Buru																			—	.11
Lombok																				—

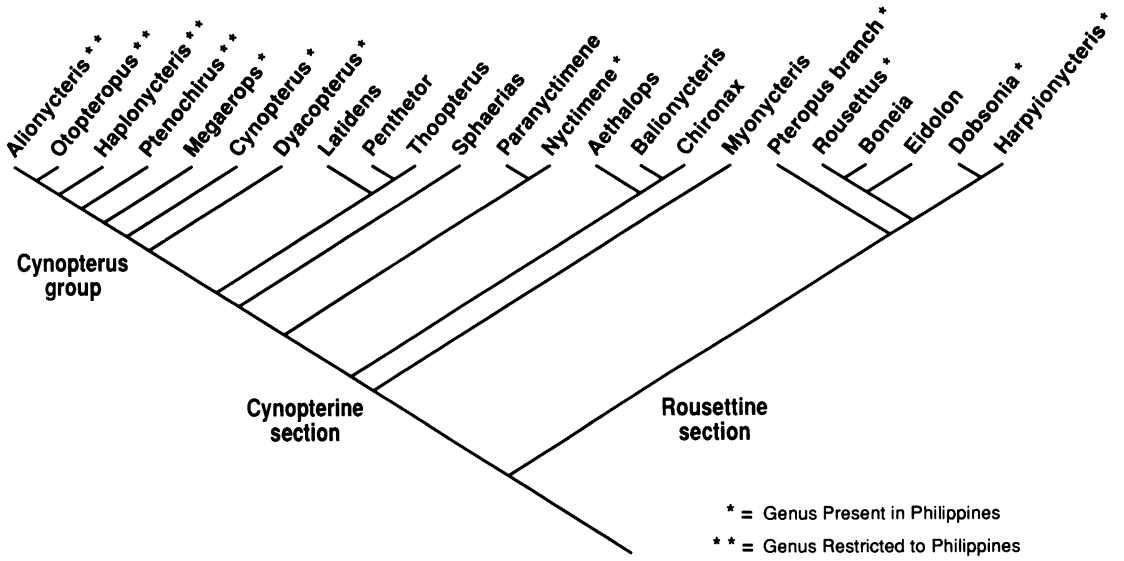

Fig. 5. Andersen's (1912) assessment of phylogenetic relationships of fruit bats known from the Philippines and their relatives, as updated by Rickart et al. (1989).

models on the basis of their predictions in this case.

The final point where a geological vicariance event might have taken place is between Mindanao and Borneo, along the Sulu Archipelago. There are several species that are shared by Mindanao and Borneo that are not widespread (e.g., *Megaerops wetmorei*; table 8), and one species pair, *Eonycteris major/ E. robusta.* Once again, there is a weak pattern, but geological evidence does not support a continuous connection of land in the past (see Study Area and Heaney, 1986), and the predicted pattern is the same in the vicariance and equilibrium models.

RATES OF COLONIZATION: Several circumstances allow documentation of rates of colonization within defined limits. The first of these involves Krakatau, where the entire fauna was extirpated in 1883. The fruit bat fauna 100 years later was five species (Hill, 1983). It is interesting to note that the five species (Appendix) are all associated with disturbed habitat, rather than primary forest (Boonsong and McNeely, 1977; Payne et al., 1985).

A second set of islands in the Philippines provides rather different estimates. Camiguin, an active volcano that lies 8 km north of Mindanao, is between about 100,000 and 1 million years old, and has at least six species of fruit bats (although current inventories are probably incomplete; Heaney, 1984b). These age estimates yield a range of one event per 17,000 years to one event per 170,000 years. Negros, a larger island that is between 1 and 4 million years old and was 15 km from Greater Mindanao during the Pleistocene, has 14 species (Heaney and Heideman, 1989). These age estimates yield a range of estimates of one event per 70,000 years to one event per 280,000 years. It should be noted, however, that Negros supports a fauna that is typical for an island of its size (i.e., it is at the "saturation point" [terminology of MacArthur and Wilson, 1967]), and one would not expect recent dispersal to result in success as often as when the island was depauperate. Likewise, Camiguin is incompletely known, and the figures given represent minimum estimates. I suggest that actual rates of colonization in the Philippines reach at least the more rapid figures given here (i.e., on the order of one event per 25,000 years), and they

TABLE 8

List of Nonendemic Genera of Philippine Fruit Bats, with Notation of the Closest Relative and the Location of that Relative's Occurrence

(Where sister species are known, these are indicated)

Philippine taxon	Closest relative	Nearest occurrence	Source
Acerodon	*Acerodon*	Sulawesi	Musser et al., 1982
Cynopterus	*Cynopterus*	Widespread (Borneo)	Hill, 1983
Dobsonia chapmani	*Dobsonia exoleta*	Sulawesi	Heaney, unpubl.
Dyacopterus	*Dyacopterus*	Borneo	Hill, 1983
Eonycteris robusta	*Eonycteris major*	Borneo	Heaney, unpubl.
Harpyionycteris whiteheadi	*Harpyionycteris celebensis*	Sulawesi	Peterson and Fenton, 1970
Macroglossus	*Macroglossus*	Widespread (Borneo)	Hill, 1983
Megaerops	*Megaerops*	Borneo	Payne et al., 1985
Nyctimene rabori	*Nyctimene cephalotes*	Sulawesi	Heaney and Peterson, 1984
Pteropus speciosus	*Pteropus griseus*	Sulawesi	Klingener and Creighton, 1984
Pteropus hypomelanus and *P. vampyrus*	*Pteropus*	Widespread (Borneo)	
Rousettus	*Rousettus*	Widespread (Borneo)	Rookmaaker and Bergmans, 1981

could be substantially more rapid, as indicated by the case of Krakatau. Tests could be made by examining more of the geologically young oceanic islands.

RATES OF EXTINCTION: Little information is currently available that might allow precise documentation of rates of extinction. Such estimates depend either on fossil specimens (e.g., Morgan and Woods, 1986), which are lacking in the Philippines, or on comparison of species-area curves for land-bridge islands and mainland (or equivalent reference areas; e.g., Heaney, 1986), which is not possible because of lack of information (e.g., from a series of forest reserves on Mindanao for comparison with Greater Mindanao land-bridge islands).

However, two approaches yield crude estimates. First, the absence of two species from a small island in the Mindanao land-bridge group provides one estimate. Two species that are abundant on every other island where we have worked (*Haplonycteris fischeri* and *Ptenochirus minor*) are absent from Maripipi (22 km^2), the only island under 500 km^2 that we have sampled (see Methods). If we assume that these species were present when Maripipi was isolated from Mindanao about 12,000 years ago, as seems likely, then extinction on this very small island has produced an extinction rate of at least one event per 6000 years. It is of interest to note that these two species are strongly associated with primary forest, and not with disturbed habitat (Heaney et al., 1989).

Second, the data inherent in the regression statistics for the Philippine fruit bats (regression A in table 4) allow another approach. A hypothetical island of 100 km^2 that was part of, for example, Greater Mindanao typically would now have 10 species. Mindanao now has 17 species, but I estimate that an area of 100 km^2 on Mindanao may have only about 14 (the number taken at a single locality on Negros; Heideman and Heaney, 1989). This suggests a loss of about 29% since the end of the Pleistocene about 15,000 years ago, or four species in 15,000 years, equal to roughly one species per 4000 years.

That the two estimates are roughly similar indicates that the true value is likely to be in the range of one extinction per 4000–6000

years on rather small islands. It should be noted that the examples involve small islands that have been attached to Mindanao, a species-rich source (i.e., they were "supersaturated" at the time of isolation), and extinction on such supersaturated land-bridge islands has been shown to be an area-dependent phenomenon for most mammals (e.g., papers in Case and Cody, 1983; Diamond and Case, 1986; Heaney and Patterson, 1986). Extinction on "undersaturated" oceanic islands is predicted to be far less common.

The similarity of estimates for rates of colonization and extinction given here (one per 25,000 years and one per 5000 years, respectively) suggests that there is potential for significant interaction between these processes, resulting in continuing turnover in the fauna, in the sense of MacArthur and Wilson (1967). If this is the case, that is, if extinction is regularly followed by colonization, then the rates of each process may be higher than estimated here. Documentation of turnover could be conducted either by direct observation (if the estimates from Krakatau are typical), by the use of fossils (e.g., Morgan and Woods, 1986) if fossil-bearing deposits can be found, or by analysis of compensatory effects, as described by Lomolino (1986). The presence in the Philippines of many endemic species and several genera indicates that turnover is not common within the Philippine archipelago as a whole.

COMPARISON WITH NONVOLANT MAMMALS

SPECIES RICHNESS AND ISLAND AREA: The relationship between island area and species richness of fruit bats in the Philippines is fairly consistent, with area accounting for 86% of the total variation in species richness (fig. 3; table 4). This differs markedly from nonvolant mammals on the same set of islands in three conspicuous ways. First, there is much less consistency among nonvolant mammals, with faunas on geologically young, isolated islands (line C in fig. 3; table 4) having substantially fewer species than those on islands of comparable size among the geologically old islands in the Luzon and Mindanao groups (line B in fig. 3; table 4). Second, there is no evidence that fruit bat faunas in the Philippines are depauperate relative to those on the Sunda Shelf, as is the case with nonvolant mammals (Heaney, 1986). Third, the slopes of the regression lines for both types of nonvolant faunas (lines B and C in fig. 3) are much steeper than among the fruit bats, as is typically the case (Lawlor, 1986).

These differences in pattern imply two differences in dynamics of the fruit bat faunas relative to the nonvolant mammal faunas. First, it should be noted that the relatively steep slope for the nonvolant mammal faunas on the Luzon and Mindanao island groups is due to post-Pleistocene isolation and extinction on the smaller islands of the groups (Heaney, 1986). The shallow slope for the fruit bat faunas on this set of islands suggests two hypotheses: either lower extinction rates on the small islands are experienced by fruit bats than by nonvolant mammals, or there is periodic recolonization by dispersing fruit bats from larger islands. These two hypotheses could initially be tested by examining patterns of genetic variation; if small-island populations of bats are genetically different from those on adjacent, more species-rich islands (when both were part of the same Pleistocene island), then the likelihood of complete post-Pleistocene isolation would be high. If no genetic differences exist, this would be weak evidence of continued gene flow, because one would expect differentiation in the absence of gene flow, although genetic differentiation might not occur if selection, mutation, and drift are absent. It should be noted that these are not exclusive hypotheses, i.e., both processes might be present, and interact (e.g., Lomolino, 1986).

The second implied difference in processes lies in the observation that at least some geologically young, isolated oceanic islands that have been colonized by few nonvolant mammals have been colonized by many fruit bat species. For example, Negros has only eight species of indigenous nonvolant mammals, which is 40% of the 20 species that would be expected on an island of its size in the Mindanao group (Heaney, 1986). In contrast, Negros has 14 species of fruit bats, which is almost precisely on the general species/area regression line for Philippine fruit bats (fig. 3). Unfortunately, the fruit bat faunas of other geologically young, isolated islands (such

as Camiguin, Mindoro, and Sibuyan) are incompletely known and cannot be included in this quantitative analysis. However, all of these islands are known to support at least moderately large fruit bat faunas (6, 8, and 8, respectively; Heaney, 1984b and unpubl. data) and seem not to be markedly depauperate. Thorough inventories of the fruit bats on these islands would be required to obtain quantitative evidence of rates of colonization and to test for evidence of reduced species richness on such islands, so that differences in the origin and maintenance of patterns of bat species richness between these geologically young, isolated oceanic islands and the older Mindanao/Luzon group islands may be determined.

Data presented above indicate that species richness of fruit bats in the Philippines exhibits a strong association with island area. This suggests the hypothesis that two variables strongly correlated with area—habitat diversity and total biomass of resources—may play a strong role in determining the ability of a given island to support viable populations of these bats. Islands that are moderately arid, such as Timor, have reduced species richness; because aridity probably increases seasonality and reduces productivity of the fruits on which these bats depend, this is concordant with the suggestion that size of resource base influences species richness. Testing of this hypothesis could be carried out by comparing additional wet islands, such as others in the Philippines and near New Guinea, with dry islands in the Lesser Sunda Islands.

A second factor that appears to influence species richness is recency of origin. The presence of a fauna of reduced species richness on Krakatau implies that development of a fruit bat fauna is impeded by recent origin, certainly on the scale of 100 years. This might be due to either or both of two factors: vegetation that will support the bats must take some time to develop, and the bats may be recolonizing as rapidly as the flora will support them; or the relatively narrow sea channels (about 45 km to both Java and Sumatra) may nevertheless be sufficient to impede colonization on a 100-year time scale. These hypotheses are nonexclusive, i.e., both could be operating simultaneously. The importance of the first factor could be investigated by studying bats on a volcano with a history similar to that of Krakatau but located on a continent or species-rich island, if such exists.

ENDEMISM AND ISLAND AREA: The smallest island in the study area that is known to support an endemic species of fruit bat is Panay (12,300 km^2). Islands as small as 229 km^2 (Tawitawi) are known to support endemic nonvolant species, and islands as small as 47 km^2 (Ilin) may do so (the species in question may also occur on Mindoro; Heaney, 1986). On the Sunda Shelf, no island smaller than Java (125,628 km^2) supports endemic species of either fruit bats or nonvolant mammals; this threshold is an order of magnitude larger than in the Philippines. Additionally, there is a significant correlation between island area and the number of endemic species among nonvolant mammals in the Philippines and on the Sunda Shelf (fig. 5 in Heaney, 1986), but there is no such correlation among fruit bats from the same islands. These data indicate either that fruit bat populations require larger areas to support viable populations than do nonvolant species, and therefore small, isolated bat populations do not persist long enough for speciation to occur; or that gene flow is typically high enough to inhibit speciation; or both. The fact that endemic species occur on smaller islands in the Philippines than on the Sunda Shelf suggests that historical isolation (which is greater in the Philippines) is a major contributing factor, supporting the gene-flow hypothesis. If this hypothesis is correct, then there should be endemic species of fruit bats yet to be discovered on small but isolated islands in the Philippines and elsewhere.

INTRAREGIONAL PATTERNS OF GEOGRAPHIC DISTRIBUTION: Both fruit bats and nonvolant mammals show high levels of endemism in the Philippines, with 14 of 23 fruit bat species (61%) and 90 of 118 nonvolant species (76%) unique to the archipelago. However, two similarities and differences are subsumed within these general figures.

First, both groups exhibit distributions strongly correlated with the extent of Pleistocene islands, but the degree of correspondence differs. For example, seven (30%) of the bat species occur on only one of the Pleistocene islands, whereas 91% of the murid

rodent species occur on single Pleistocene islands (Heaney and Rickart, 1990). From another perspective, 7% and 12% of the fruit bats on Greater Luzon and Greater Mindanao are endemic, respectively (table 2), whereas 72% and 79% of the nonvolant mammals on those islands are endemic. Thus, the fruit bats show the same pattern of distribution of endemic species, but differ in the degree of endemism.

Second, although the fruit bats have much lower levels of endemism at the level of individual islands than do nonvolant mammals, they have nearly equal levels of endemism when the archipelago is considered as a whole (61% versus 76%, respectively). In other words, most endemic fruit bats are distributed throughout the archipelago rather than restricted to single historically defined regions (the Pleistocene islands). This again implies substantially greater dispersal ability than that possessed by the great majority of nonvolant mammals.

QUANTITATIVE INTERREGIONAL SIMILARITIES: Although the islands used in this study and in my earlier (1986) study of nonvolant species are not identical, there is enough overlap to make several illuminating comparisons.

First, it is apparent that overall similarity values for fruit bat faunas are higher than among nonvolant mammals (table 7; tables 6 and 7 in Heaney, 1986) as a consequence of the larger number of widespread species, as discussed above.

Second, in both cases the Philippine faunas on the oceanic islands are distinct from those on the Sunda Shelf (fig. 4). Unfortunately, the fruit bat faunas of the Palawan group are incompletely known (especially lacking good samples from primary forest), so that we do not know if they cluster with the Sunda Shelf faunas as the result of a middle Pleistocene land bridge to Borneo, as do the nonvolant mammals (Heaney, 1986).

RATES OF COLONIZATION: The rough estimate of colonization rates within the Philippine fruit bat fauna of at least one event per 25,000 years is at least 10 times that for nonvolant mammals, for which a rate of one event per 250,000–500,000 years has been estimated (Heaney, 1986).

Detection of the impact of isolation (i.e., of the effect of distance on the rate of colonization and thereby on species richness) is certainly in part a matter of time scale. No effect of isolation among fruit bats is evident from species-richness relationships within the Philippines, which implies that, given the ages of the islands sampled, distance has had a negligible impact. However, few of the geologically young oceanic islands that are needed for temporal refinement have been thoroughly inventoried. Reduced species richness on Buru implies that some isolation effect may be present, although the degree of reduction (30%; 9 species rather than the 13 predicted for an equal-sized island in the Philippines) is less than among nonvolant mammals, where reduction of 60%–80% is common (Lawlor, 1986). I suggest that the best test for effects of isolation on species richness would be in the Philippines, where several geologically young oceanic islands may show such effects over a short time span, and further east in the Pacific, where islands of greatly increasing isolation lie to the east of species-rich New Guinea. Preliminary description indicates that isolation effects are present (Phillips, 1968), but quantitative examination has not been attempted.

RATES OF EXTINCTION: Comparison of extinction rates among fruit bats and nonvolant mammals within the Philippines can be made only with limited precision because of limited data, but a single example is instructive. As indicated above, on a hypothetical island of 100 km^2, extinction was estimated to be four species in 15,000 years (29%; ca. one per 3700 years). A similar calculation for nonvolant mammals, using the regression for the Luzon and Mindanao groups (equation B, table 4), indicates that nine species typically will be present. Mindanao has 25 species, and I estimate that an area of 100 km^2 on Mindanao would have at least 16 species (based on published surveys and on general habitat associations); this indicates extinction of seven species (44%) in 15,000 years on the hypothetical island, or one extinction per 2100 years, or about 75% higher than among fruit bats. Even though this is a lower rate than on the continental shelf (where the initial number of species is much greater; Heaney, 1986),

it is still substantially higher than among bats. More precise data are badly needed, but a trend is apparent.

CONCLUSIONS

The exceptional diversity of island size, geological history, and degree of isolation, and the unique combination of these factors, make Indo-Australia, and especially the Philippines, an ideal place to investigate problems in evolutionary biogeography. This diversity is particularly critical in attempting to move from a descriptive phase of biogeography to one of quantitative investigation of processes that produce the evident patterns.

The picture that emerges from these analyses of Indo-Australian fruit bats is one of a fauna that is dynamically evolving, with colonization, extinction, and phylogenetic diversification all playing significant roles in determining patterns of species richness and distribution. Each of these processes, and the patterns that each produces, is interwoven with the others in complex interactive fashion. It is apparent that no single process can be fully understood in the absence of consideration of the others, and that one of the principal challenges to investigators of these processes will be to devise methods that will allow quantitative determination of the manner and degree to which the processes interact by insightful use of the exceptional natural variation in geological and geographical circumstances in the Indo-Australian region.

This preliminary assessment indicates that interisland colonization is a moderately common phenomenon among these bats, with many oceanic islands showing no evidence of a reduction in species richness, and only geologically very young (Krakatau), quite isolated (Buru, and perhaps Seram and Halmahera), or arid (Timor) islands showing evidence of reduced species richness. The presence of several very widespread species strongly reinforces this interpretation. Nevertheless, the presence of many localized endemics and at least one geographically restricted but speciose monophyletic clade on an oceanic island group (the Philippine dwarf fruit bats) implies that this colonization ability does have limits. Quantitative assessment of rates of colonization, and the ecological and geographic circumstances of such colonization, should be a major future research goal.

The impact of extinction among these bats appears to be much less than among nonvolant species in the same areas. The very shallow slope of the species-area curve among Philippine fruit bats indicates that extinction on land-bridge islands has been quite slight, whereas among the nonvolant species the slope is quite steep due to the often overwhelming extinction of species on small islands. Nevertheless, the conspicuous absence of fruit bats of two species on at least one island (Maripipi) gives evidence that extinction does take place. The inventory of additional small land-bridge islands and of reference areas on source islands (e.g., Luzon and Mindanao) will be important for further assessment of this pattern, and the discovery and study of fossil material would add a crucial temporal component to interpretations of extinction rates and possible causes. Evidence of turnover in these faunas should especially be sought.

Speciation is clearly a substantial contributor to current patterns of species richness and distribution. This is true both among individual species whose ancestors reached the Philippines from outside sources without subsequent diversification (e.g., *Dobsonia chapmani, Eonycteris robusta, Harpyionycteris whiteheadi,* and *Nyctimene rabori*) and among the members of the diverse radiation of Philippine dwarf fruit bats that is composed of at least five species. The role of geological vicariance events is currently ambiguous, with little evidence that such events took place, and the patterns they might produce are only weakly evident and subject to other interpretation. Among Philippine fruit bats, it appears that speciation is probably more intimately related to colonization than to vicariance events, both in the presence of endemic species whose sister species occur in other regions that were never contiguous and in the sympatric occurrence of four of the five members of the endemic dwarf fruit bat group. Further study of phylogenetic relationships among Philippine fruit bats and those of ad-

jacent regions will refine our understanding of the process of phylogenetic diversification, and the integration of more information on geological history, especially in areas where geological vicariance phenomena are more certain to have taken place and more common, will allow more complete assessment of the general importance of this process.

I began this paper by posing the general hypothesis that the biogeographic patterns of fruit bats are fundamentally the same as those of nonvolant mammals, in spite of the apparently greater vagility of bats. The data presented in this paper lead me to accept this hypothesis with regard to the Philippine fauna, but with an important proviso. It is true that the bats display the same patterns of, for example, faunal similarity and concordance with the extent of Pleistocene islands that are exhibited by nonvolant mammals. Furthermore, the same processes of colonization, extinction, and phylogenetic diversification are identified as being present in both the bat fauna and nonvolant mammal fauna, and as being influenced by the same factors of isolation, island area, and geological age (among others). However, it is apparent that the rates of these processes differ greatly between the two groups, with the bats having much greater rates of colonization and lower rates of both extinction and localized speciation. These differences are likely to be due precisely to the greater vagility of bats. I conclude that the underlying processes involved in determining patterns of fruit bat species richness and distribution are indeed the same as those of other mammals, but that bats are unique among mammals in the rates of these phenomena and hence in the dynamics of their biogeographical evolution.

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APPENDIX

Lists of fruit bats recorded from Ambon, Buru, Halmahera, Krakatau, Lombok, New Guinea, Seram, Sulawesi, and Timor are presented below. Asterisks indicate species known only from an adjacent small island, and presumed to occur on the islands listed here.

AMBON: *Dobsonia moluccensis, D. viridis, Macroglossus minimus, Nyctimene cephalotes, N. minutus, Pteropus chrysoproctus, P. melanopogon, P. temmincki, Rousettus amplexicaudatus, Syconycteris australis.* Sources: Laurie and Hill, 1954; Rookmaaker and Bergmans, 1981; Honacki et al., 1982; Rozendaal, 1984.

BURU: *Dobsonia moluccensis, D. viridis, Macroglossus minimus, Nyctimene cephalotes, N. minutus, Pteropus chrysoproctus, P. melanopogon, P. ocularis, P. temmincki.* Sources: Laurie and Hill, 1954; Rookmaaker and Bergmans, 1981; Honacki et al., 1982; Rozendaal, 1984.

HALMAHERA: *Dobsonia crenulata, D. moluccensis*, Macroglossus minimus, Nyctimene albiventer, N. aello, Pteropus caniceps, P. conspicillatus, P. hypomelanus, P. personatus, Rousettus amplexicaudatus, Syconycteris carolinae, Thoopterus nigrescens*.* Sources: Laurie and Hill, 1954; Rozendaal, 1984; specimens in USNM.

KRAKATAU: *Cynopterus horsfieldi, C. sphinx, C. titthaecheilus, Macroglossus sobrinus, Rousettus amplexicaudatus.* Source: Hill, 1983: 121, 137.

LOMBOK: *Acerodon mackloti, Aethalops alecto, Cynopterus brachyotis, C. horsfieldi, C. titthaecheilus, Dobsonia peronii, Eonycteris spelaea, Macroglossus minimus, Pteropus alecto, P. lombocensis, P. vampyrus, Rousettus amplexicaudatus, R. leschenaultii.* Source: Kitchener et al., 1990.

NEW GUINEA: *Aproteles bulmerae, Dobsonia minor, D. moluccensis, Macroglossus minimus, Nyctimene aello, N. albiventer, N. cephalotes, N. cyclotis, N. draconilla, Paranyctimene raptor, Pteropus alecto, P. conspicillatus, P. hypomelanus, P. macrotis, P. pohlei*, P. neohibernicus, P. scapulatus, Rousettus amplexicaudatus, Syconycteris australis, S. hobbit.* Sources: Laurie and Hill, 1954; Koopman, 1979; Koopman, 1982; Ziegler, 1982; Flannery, 1990.

SERAM: *Dobsonia moluccensis, D. viridis, Macroglossus minimus, Nyctimene cephalotes, N. minutus, Pteropus chrysoproctus, P. melanopogon, P. ocularis, P. temmincki, Rousettus amplexicaudatus, Syconycteris australis.* Sources: Laurie and Hill, 1954; Rookmaaker and Bergmans, 1981; Honacki et al., 1982; Rozendaal, 1984.

SULAWESI: *Acerodon celebensis, Boneia bidens, Chironax melanocephalus, Cynopterus brachyotis, Dobsonia exoleta, D. minor, D. viridis, Eonycteris spelaea, Harpyionycteris celebensis, Macroglossus minimus, Neopteryx frosti, Nyctimene cephalotes, N. minutus, Pteropus alecto, P. caniceps, P. griseus, P. hypomelanus, Rousettus amplexicaudatus, R. celebensis, Stylocteníum wallacei, Thoopterus nigrescens.* Sources: Hill, 1983; Rozendaal, 1984; Musser, 1987; Bergmans and Rozendaal, 1988.

TIMOR: *Acerodon mackloti, Cynopterus titthaecheilus, Dobsonia peroni, Eonycteris spelaea, Macroglossus minimus, Nyctimene cephalotes, Pteropus griseus, P. vampyrus, Rousettus amplexicaudatus.* Source: Goodwin, 1979.

Bats (Mammalia: Chiroptera) from the Togian Islands, Sulawesi, Indonesia

J. E. HILL[1,2]

ABSTRACT

Members of the Oxford University Expedition of 1987 to the Togian Islands, off north-central Sulawesi in Indonesia, collected and recorded a number of bats from several of the islands of this small archipelago. The chiropteran fauna of the Togians hitherto was poorly known. In this paper I report and briefly discuss the species encountered, many of which are reported from the islands for the first time. As might be expected from the close proximity of the islands to Sulawesi itself, their bat fauna is a reflection of that found on the adjacent parts of this much larger island. Bats appear to be relatively common on the Togian Islands, which have numerous areas of forest and cultivation and a proliferation of caves, providing some variety of habitat and especially of roosting sites.

INTRODUCTION

The Togian Islands (Kepulauan Togian) (fig. 1) lie at 0°20'S, 122°00'E in the Gulf of Tomini, between (but close to) the main body of Sulawesi itself and the northern arm of that island. The archipelago consists of a cluster of six generally larger and closely adjacent islands (Batu Daka, Togian, Malenge, Talata Koh, Walea Kodi, and Walea Bahi), none more distant than about 10 km from another and usually less, with outliers some 20–30 km to the northwest (Una Una) and southeast (Pulau Puah). There are many smaller islands and islets in the main group, and coral reefs are found everywhere. At their nearest point, the islands are little more than 25 km from north-central Sulawesi and are separated from each other and from Sulawesi itself only by shallow seas. The principal group consists of reef limestone with numerous caves, some subject to tidal influx. Mangrove forests occur on most coasts; otherwise, on poorer soils, the forest is sparse, but elsewhere, under better conditions, it is more diverse, with many larger trees. Some logging is carried out on Batu Daka and Togian, and large patches have been cleared in many parts of the islands for plantations, chiefly of coconuts and bananas.

There appears to have been no previous systematic survey of the bats of the Togian Islands, although a few specimens have been recorded, principally from Togian or Malenge. The Oxford University Expedition of 1987 to the Togian Islands had as its principal objective a survey of a variety of caves and their chiropteran and invertebrate faunas. During the period from early August to late September, 17 caves were examined in detail and visits were made to 4 others. A total of 227 bats was identified and measured in the field, of which the representative series reported here was sent to the British Museum (Natural History), London, for confirmation of their identities, for further study, and as voucher specimens. In addition, numerous bats were observed in caves and sometimes identified; the majority of those studied and collected were from such sites, with relatively few being obtained above ground. A com-

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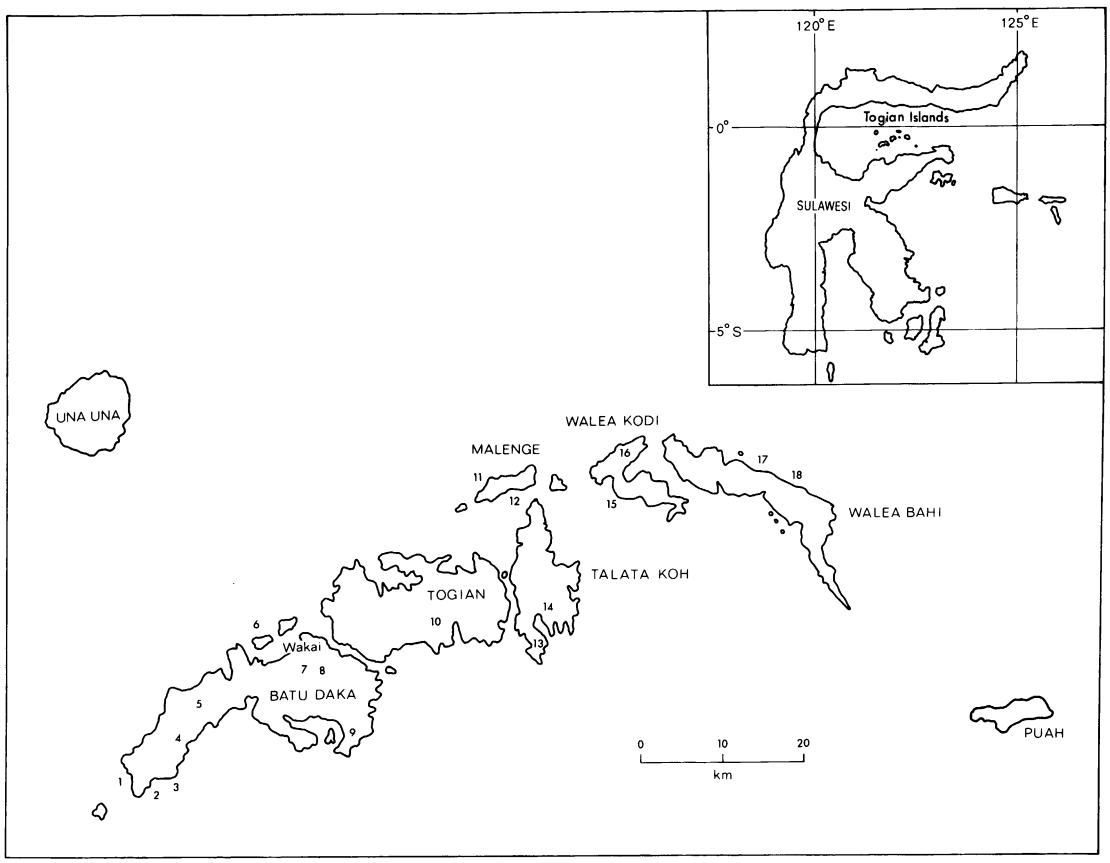

Fig. 1. The Togian Islands, Sulawesi, Indonesia. Cave locations where bats were examined and obtained by the Oxford University Expedition, 1987. **1.** Bomba (on small island a short distance offshore from Batu Daka Island). **2.** Kuling Kenari 2. **3.** Kuling Kenari 1. **4.** Lindu. **5.** Tumbuluwa. **6.** Bungi. **7.** Tanimpo Gorge (possibly a former cave with collapsed roof). **8.** Tanimpo. **9.** Masapi. **10.** Benteng. **11.** Kadoda. **12.** Malenge. **13.** Layang Sea. **14.** Layang Land. **15.** Toani. **16.** Populii Forest 2. **17.** Dingin. **18.** Kalapuang. (After Owen et al., 1987.)

prehensive account of the Expedition has been issued (Owen et al., 1987), with details of the terrain and of the caves and their fauna, and with an assessment of the bat population and its local distribution and of any relevant factors such as human interference that may affect the caves or the bats that they harbor.

Methods

Forearm lengths given in the present paper are in most cases those established (with dial calipers) in the field, and as such have been drawn from the list of specimens examined that is given in the account of the Expedition (Owen et al., 1987), to take advantage of the larger series so available. Weights (taken with a Pesola balance) where recorded here are from the same source. Dimensional measurements are in millimeters, weights in grams. Specimens in the collection are preserved in alcohol. Some will be deposited in the Museum Zoologicum Bogoriense, Bogor, Indonesia, the remainder being retained in the British Museum (Natural History), London.

Acknowledgments

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Stuart Strathdee, Kate G. Lonsdale, and Pingkan Jans—whose efforts in the field assembled the specimens and data upon which this paper is based, and whose Expedition Report (Owen et al., 1987) has been invaluable in preparation of this report. Facilities at the British Museum (Natural History) have been generously provided by the Keeper of Zoology, and I am indebted to the staff of the Mammal Section and especially to P. D. Jenkins for numerous courtesies. I am also grateful to T. A. Griffiths of Illinois Wesleyan University, Bloomington, and to G. G. Musser of the American Museum of Natural History, New York, for their editorial assistance.

SYSTEMATIC SECTION

Rousettus amplexicaudatus amplexicaudatus (E. Geoffroy, 1810)

Pteropus amplexicaudatus E. Geoffroy, 1810: 96, pl. 4 (Timor Island, Lesser Sunda Islands).

Batu Daka: ♂121, Tumbuluwa Cave, short walk inland from northern coast.

Malenge: ♂116, Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

These specimens are referred to *R. a. amplexicaudatus* after Bergmans and Rozendaal (1988), who allocated numerous others from Sulawesi and from Lembeh Island (0°26′S, 125°13′E) to this subspecies. The right anterior upper premolar (PM2) and both last upper molars (M2–M2) are lacking from specimen 116. Length of forearm (121) 79.3, (116) 79.6.

Rousettus celebensis Andersen, 1907

Rousettus celebensis Andersen, 1907: 509 (Mount Masarang, northern Sulawesi, 350 ft).

Batu Daka: ♂139 (also 4♂♂, 4♀♀ examined but not retained), Lindu Cave, short walk inland from southern coast.

Malenge: ♂107, Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

Talata Koh: ♂♂30, 31 (also 5♂♂, 11♀♀ examined but not retained), Layang Sea Cave, on peninsula on southern coast; 5♂♂, 2♀♀ (examined but not retained), Layang Land Cave, short walk inland from southern coast.

Walea Kodi: 3♂♂, 14♀♀ (examined but not retained), Toani Village, short walk inland from southern coast; ♂, ♀ (examined but not retained), Populii Village; 5♀♀ (examined but not retained), Populii Forest Cave 2, near Populii Village.

Walea Bahi: ♀227, Pasokan Village, on coast; ♂, ♀ (examined but not retained), Dingin Cave.

An example (BM(NH) 1981.1075) of *R. celebensis* lacking the right last upper molar (M2) and the second and last left lower molars (m2, m3) was reported by Hill (1983): the right anterior upper premolar (PM2) is missing from specimen 107. Measurements of specimens from the Togian Islands: length of forearm in ♂♂ (23) 67.8–76.6 (72.7), in ♀♀ (36) 67.5–76.1 (72.4); weight in ♂♂ (23) 46.7–72.0 (62.7), in ♀♀ (35) 34.5–67.0 (52.3), field measurements.

Styloctenium wallacei (Gray, 1866)

Pteropus wallacei Gray, 1866: 65, fig. 1 (Makassar, southern Sulawesi).

Walea Kodi: ?181, Populii Village.

Tate (1942) reported *S. wallacei* from Malenge. Length of forearm in the example from Walea Kodi 98.5; in two specimens (♂, ♀, BM(NH) 1987.177–178) from west of Kotamabagou, northern Sulawesi, at 0°31′N, 123°58′E, the forearms measure 93.8 and 95.1. The specimen from Walea Kodi is cranially a little smaller than specimens from northern Sulawesi reported by Bergmans and Rozendaal (1988) or one from central Sulawesi recorded by Hill (1983). Cranial measurements of the example from Walea Kodi: greatest length of skull 47.9; condylobasal length 46.4; palatal length 25.5; rostral width 18.1; least interorbital width 6.1; least postorbital width 5.6; zygomatic width 26.2; width of braincase 17.9; mastoid width 17.7; C1–C1 (alveoli) 8.6, (cingula) 9.2; M1–M1 (alveoli) 12.8, (crowns) 13.2; M2–M2 (alveoli) 11.6, (crowns) 11.9; C–M2 18.2; length complete mandible from condyles 35.3; length right ramus from condyle 37.4; c–m2 18.9.

Dobsonia viridis crenulata Andersen, 1909

Dobsonia crenulata Andersen, 1909: 532 (Ternate Island, Molucca Islands).

Batu Daka: ♂126 (also 2♂♂, ♀ examined but not retained), Kuling Kenari Cave 2, on southwestern coast; 3♂♂, 2♀♀ (one juvenile) (examined but not retained), Bomba Cave, on small island off southwestern coast, short distance offshore from

Bomba Village; ♀136 (also ♂, ♀ examined but not retained), Lindu Cave, short walk inland from southern coast; 2♀♀ (examined but not retained), Masapi Cave, opposite Bambu Island.

Talata Koh: ♂♂48, 50 (also ♀ examined but not retained), Layang Sea Cave, on peninsula on southern coast; ♂59 (also 3♀♀ [one juvenile] examined but not retained), Layang Land Cave, short walk inland from southern coast.

These specimens have rather heavier canines and slightly longer and wider last upper premolars (PM4), first upper molars (M1), and first and second lower molars (m1–m2) than those from central Sulawesi referred questionably to *D. v. viridis* by Hill (1983). In these respects they agree with *crenulata*, previously recorded from the Togian Islands (Una Una, Malenge) by De Jong and Bergmans (1981). Length of forearm in specimens reported above: ♂♂ (10) 108.4–132.8 (118.9), ♀♀ (9) 113.1–128.2 (120.0), field measurements.

Cynopterus brachyotis brachyotis (Müller, 1838)

Pachysoma brachyotis Müller, 1838: 146 (River Dewei, Borneo).

Cynopterus minor Revilliod, 1911: 517 (Lambuja, southeastern Sulawesi).

Batu Daka: ♀15, Bungi Cave, on small island off northern coast.

Walea Kodi: ♂♂170, 172, Toani Village, short walk inland from southern coast; ♀179, Populii Village.

Length of forearm (♂♂170, 172, ♀179) 59.5, 59.8, 59.2; weights, field measurements, 28.0, 26.5 (dead weight), 31.5 (pregnant, dead weight). Specimens from northern Sulawesi in the collections of the British Museum (Natural History) have forearm lengths in ♂♂ of (3) 60.0–64.1 (61.6), in ♀♀ (2) 60.1, 61.1, and from central Sulawesi the forearm length in ♂♂ is (21) 57.2–64.1 (60.7), in ♀♀ (12) 60.0–63.3 (60.9), whereas specimens from the Banggai Islands have forearm lengths in ♂♂ of (3) 60.0–63.3 (61.6). All agree in forearm length with further examples from northern Sulawesi and the Banggai Islands recorded by Bergmans and Rozendaal (1988) and are similarly generally smaller than specimens from southern Sulawesi and the Sangihe Islands reported by these authors.

Emballonura nigrescens papuana Thomas, 1914

Emballonura papuana Thomas, 1914: 443 (Wakatimi, River Mimika, southwestern West Irian, New Guinea).

Togian: ♂27, ♀29 (also ♂, ♀ examined but not retained), Benteng Mountain, 300 m.

Length of forearm (4) 31.4–34.2 (32.9), field measurements.

Emballonura alecto alecto (Eydoux and Gervais, 1836)

Vespertilio (*Nycticeius*) *alecto* Eydoux and Gervais, 1836: 7 (Manila, Luzon Island, Philippine Islands).

Batu Daka: ♂♂124, 127, 130, Kuling Kenari Cave 2, on southwestern coast; 4♂♂, 3♀♀ (examined but not retained), Masapi Cave, opposite Bambu Island.

Togian: ♂25, Benteng Mountain Cave.

Walea Kodi: ♂157 (also 2♀♀ examined but not retained), Toani Cave, short walk inland from southern coast; ♀188, Populii Forest Cave 2, near Populii Village.

These specimens agree closely in size with examples from central Sulawesi reported by Hill (1983) and from northern Sulawesi by Hill and Rozendaal (1989). Length of forearm (15) 44.7–47.8 (45.9), field measurements. Cranial dimensions of specimen 127: greatest length of skull 15.0; condylobasal length 13.9; condylocanine length 13.2; width rostral swellings —; least interorbital width —; least postorbital width 3.1; zygomatic width 8.9; width of braincase 6.6; mastoid width 7.8; C1–C1 (alveoli) 3.6, (cingula) 3.6; M3–M3 (alveoli) 6.3, (crowns) 6.4; C–M3 5.7; length complete mandible from condyles 10.0; length right ramus from condyle 10.5; c–m3 5.7.

Taphozous melanopogon fretensis Thomas, 1916

Taphozous melanopogon fretensis Thomas, 1916: 5 (Terutau Island, off extreme southwestern Thailand).

Walea Bahi: ♂♂194, 195, ♀♀191, 193 (also 5♂♂, 2♀♀ examined but not retained), Dingin Cave.

Specimens from the Togian Islands agree closely with the holotype and other examples

of *T. m. fretensis* otherwise distributed from the Malay Peninsula and its coastal islands to Borneo. Larger examples recorded by Hill (1983) from souther Sulawesi are similar in size to those reported by Goodwin (1979) from Timor, Lesser Sunda Islands, or to *T. m. achates* Thomas, 1915a, from Savu Island, near Timor, which probably they represent. Length of forearm (12) 60.4–64.6 (61.6), field measurements. Cranial dimensions of specimen 191: greatest length of skull 20.6, condylocanine length 19.7; least interorbital width 5.9; least postorbital width 5.1; zygomatic width 12.3; width of braincase 9.8; mastoid width 11.0; C1–C1 (alveoli) 3.9, (cingula) 4.0; M3–M3 (alveoli) 8.8, (crowns) 8.8; C–M3 8.7; length complete mandible from condyles 15.1; length right ramus from condyle 15.5; c–m3 9.5.

Rhinolophus celebensis celebensis Andersen, 1905

Rhinolophus celebensis Andersen, 1905: 83, pl. 3, fig. 4a, b (Makassar, southern Sulawesi).

Batu Daka: ♂123, ♀122, Kuling Kenari Cave 1, on southwestern coast.
Malenge: ♂113, Kadoda Cave, short walk inland from northern coast, near Kadoda Village.
Walea Kodi: ♀186, Populii Forest Cave 2, near Populii Village.

Length of forearm (4) 40.3–43.0 (41.3).

Rhinolophus euryotis tatar Bergmans and Rozendaal, 1982

Rhinolophus tatar Bergmans and Rozendaal, 1982: 170, figs. 1–5 (River Moinakom, Dumoga Nature Reserve, northern Sulawesi, 525 m, 0°41′N, 124°03′E).

Batu Daka: ♂138, Lindu Cave, short walk inland from southern coast.
Malenge: ♂78 (also ♂ examined but not retained), Kadoda Cave, short walk inland from northern coast, near Kadoda Village.
Talata Koh: ♂♂69, 70 (also 3♂♂, 7♀♀ examined but not retained), Layang Land Cave, short walk inland from southern coast.
Walea Kodi: ♂♂189, 190, Populii Forest Cave 2, near Populii Village.

Length of forearm (17) 50.0–53.3 (51.9), field measurements.

Hipposideros ater saevus Andersen, 1918

Hipposideros albanensis saevus Andersen, 1918: 380, 381 (Kai Islands, Molucca Islands).

Batu Daka: ♀♀15, 21 (juvenile) (also ♀ examined but not retained), Bungi Cave, on small island off northern coast.
Malenge: ♂♂84, 86, ♀83 (also 5♂♂, 4♀♀ examined but not retained), Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

Length of forearm (14) 37.8–40.8 (39.5), field measurements.

Hipposideros cervinus cervinus (Gould, 1854)

Rhinolophus cervinus Gould, 1854: pl. 34, letterpress ("Caves on Albany Island," Cape York, Queensland, Australia).

Batu Daka: ♂♂16, 21, ♀♀18, 19 (also 3♂♂, ♀ examined but not retained), Bungi Cave, on small island off northern coast.
Malenge: 2♀♀ (examined but not retained), Kadoda Cave, short walk inland from northern coast, near Kadoda Village.
Talata Koh: ♀62, Layang Land Cave, short walk inland from southern coast.
Walea Bahi: ♀♀218, 223 (also 6♂♂, ♀ examined but not retained), Kalapuang Cave.

These specimens agree in forearm length with those from southern and central Sulawesi reported by Hill (1983), but on the whole their forearms are slightly shorter than those of examples from northern Sulawesi measured by Hill and Rozendaal (1989). Length of forearm in specimens from the Togian Islands (16) 44.5–48.7 (46.5), field measurements.

Hipposideros diadema speculator Andersen, 1918

Hipposideros d[iadema] speculator Andersen, 1918: 381, 382 (Kalao Island, Flores Sea, south of Sulawesi).

Batu Daka: ♂4, Tanimpo Gorge Cave, near River Tanimpo, ca. 5 km southeast of Wakai (ca. 0°28′S, 121°54′E); ♀7 (also ♂ examined but not retained), Tanimpo Gorge, on route along River Tanimpo from Kamping Baru to Tanimpo Gorge Cave.

These specimens are similar in forearm length to two examples from northern Sulawesi reported by Hill and Rozendaal (1989).

Length of forearm (3) 84.6–87.2 (86.3), field measurements.

Myotis adversus moluccarum (Thomas, 1915)

Leuconoe moluccarum Thomas, 1915b: 170 (Ara, Kai Islands, Molucca Islands).

Batu Daka: ♂119, ♀118 (also ♀ examined but not retained), Tumbulawa Cave, short walk inland from northern coast; ♂5 (also 2♀♀ examined but not retained), Tanimpo Gorge Cave, near River Tanimpo, ca. 5 km southeast of Wakai (ca. 0°28′S, 121°54′E); ♂10, ♀9 (also ♂, 2♀♀ examined but not retained), Tanimpo Gorge, on route along River Tanimpo from Kamping Baru to Tanimpo Gorge Cave.

Malenge: ♂♂96, 108, ♀104 (also 2♂♂, ♀ examined but not retained), Kadoda Cave, short walk from northern coast, near Kadoda Village.

Length of forearm (15) 39.7–43.1 (41.6), field measurements.

Miniopterus australis tibialis (Tomes, 1858)

Vespertilio tibialis Tomes, 1858: 126 (Ambon Island, Molucca Islands).

Batu Daka: ♂14, Tanimpo Gorge Cave, near River Tanimpo, ca. 5 km southeast of Wakai (ca. 0°28′S, 121°54′E).

Malenge: ♂♂91, 99 (also 4♂♂, 4♀♀ examined but not retained), Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

Walea Bahi: ♂♂205, 206, ♀217 (also 3♂♂, 6♀♀ examined but not retained), Kalapuang Cave.

Length of forearm (23) 35.2–38.6 (37.1); weight (22) 4.0–6.3 (5.2), field measurements.

(?)*Miniopterus pusillus macrocneme* Revilliod, 1914

Miniopterus macrocneme Revilliod, 1914: 360, pl. 10, figs. 5, 6, 11 (New Caledonia and Loyalty Islands [Lifou Island, Maré Island]).

Malenge: 3♂♂, 2♀♀ (examined but not retained), Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

The length of the forearm in these specimens and their weight suggest that they may represent *M. p. macrocneme* Revilliod, 1914, to which they are provisionally assigned, previously recorded from southern and central Sulawesi by Hill (1974, 1983), but none was retained and this supposition cannot be confirmed. The largest examples overlap *M. medius* Thomas and Wroughton, 1909, in forearm length, but that species has yet to be reported from Sulawesi. Length of forearm (5) 40.0–43.2 (41.8); weight (5) 7.6–9.1 (8.3), field measurements.

Miniopterus tristis celebensis Peterson, 1981

Miniopterus tristis celebensis Peterson, 1981: 841, fig. 8f (Luwu, Wawondula, Sulawesi, 2°38′S, 121°21′E).

Batu Daka: ♂120, Tumbulawa Cave, short walk inland from northern coast; ♂♂1, 2, ♀6 (also ♀ examined but not retained), Tanimpo Gorge Cave, near River Tanimpo, ca. 5 km southeast of Wakai (ca. 0°28′S, 121°54′E).

Malenge: ♂109, Kadoda Cave, short walk inland from northern coast, near Kadoda Village.

Walea Bahi: ♂208, Kalapuang Cave.

This subspecies was previously known only from the type locality and from the River Ranu in central Sulawesi (Hill, 1983). Length of forearm (7) 55.5–57.2 (56.3), field measurements.

HUMAN UTILIZATION

Large or relatively large megachiropterans are evidently a regular food source in northern Sulawesi. The variety of species available in the market at Imandi, in the Domoga Valley, north of Kotamobagu, 0°35′N, 124°04′E, indicates the extent of this practice. Specimens purchased by A. J. Marshall (in British Museum [Natural History]) or recorded by Bergmans and Rozendaal (1988) from this source include much of the known megachiropteran fauna of northern Sulawesi, with representatives of *Rousettus* (*Rousettus*) *amplexicaudatus, Rousettus* (*Rousettus*) *celebensis, Rousettus* (*Boneia*) *bidens, Pteropus alecto alecto, Acerodon celebensis, Neopteryx frosti, Styloctenium wallacei, Dobsonia exoleta, Cynopterus brachyotis brachyotis, Thoopterus nigrescens, Harpyionycteris celebensis, Nyctimene cephalotes cephalotes,* and *Eonycteris spelaea rosenbergii.* Some larger microchiropterans such as *Cheiromeles parvidens* are also offered for sale at Imandi (Bergmans and Rozendaal, 1988).

Megachiropterans in the Togian Islands are similarly a food item for some of the local population, and it is possible that bats are

exported to Manado or elsewhere in northern Sulawesi, or that the islands may be visited by bat hunters from the nearby mainland.

CONCLUSION

As might be expected, the chiropteran fauna of the Togian Islands proves to be essentially the same as that of the adjacent Sulawesian mainland, most representatives apparently not differing materially from their mainland counterparts. Specimens of *Cynopterus brachyotis* from the Togian Islands are similar in size to others from mainland locations in northern and central Sulawesi, and like these are smaller than examples from the southwestern part of the island (cf. Bergmans and Rozendaal, 1988), whereas specimens of *Taphozous melanopogon* from the Togian Islands are sufficiently smaller than examples of this species from southern Sulawesi that they apparently represent a different subspecies. It is possible that some of the larger megachiropterans might well cross the relatively narrow strait separating the Togian Islands from the mainland: it seems unlikely that this channel presents an insuperable obstacle to a species such as *Acerodon celebensis* (recorded from Malenge Island by Musser et al., 1982). Similarly, interchange between islands within the Togian group seems inevitable. The gaps between several of the islands are very narrow and do not seem likely to be a barrier for many species, even of microchiropterans.

Lack of time and of suitable guides prevented any detailed survey of tree-roosting megachiropterans: known roosts are to be found on Una Una Island, on Panjang Island, off the northern coast of Batu Daka, and on a small island off Togian Island or on Togian itself. No megachiropterans were obtained outside caves other than a single example of *Styloctenium wallacei* (accidentally caught in a villager's bird trap) from Populii Village on Walea Kodi and three specimens of *Cynopterus brachyotis brachyotis,* one of these from Populii Village, the others from Toani Village, on the same island.

The many caves scattered throughout the islands evidently provide excellent refuges for a variety of cavernicolous species. Just as the forested areas of the Togian Islands may represent an extension of similar habitats in northern Sulawesi for tree-roosting megachiropterans, so the caves provide shelter for populations of the cave-roosting fruit bats *Rousettus* and *Dobsonia.* Bats considered to be *Eonycteris spelaea* were encountered during a reconnaissance visit in 1986 and by members of the expedition itself in 1987, but none was examined closely or retained, and thus the identification cannot be confirmed. Besides fruit bats, the caves also house a variety of microchiropteran species, sometimes in large numbers. The most densely populated of the caves contained probably 1500 *Rousettus* and possibly as many as 10,000 microchiropterans, other caves housing lesser but nonetheless sometimes quite substantial populations.

It is clear from the survey carried out by this expedition that the Togian Islands are an important and significant habitat for bats, with a broad representation of species and a considerable local population. Some disturbance of a few of the caves may result from the collection of swiftlet nests or guano, and fruit bats are hunted for food to an unknown but possibly as yet relatively limited extent. As Bergmans and Rozendaal (1988) pointed out, fruit bats have been hunted and eaten in northern Sulawesi for many years, if not centuries. Although in the past the fruit bat population evidently has largely withstood this pressure, the loss of rain forest and roosting sites, increasing demand, and the availability of air rifles or even shotguns to improve hunting efficiency may place the existing fauna in jeopardy.

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Neotropical Chiroptera from the Pliocene and Pleistocene of Florida

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ABSTRACT

There is a strong Neotropical influence in Florida fossil vertebrate faunas dating back to the beginning of the Great American Faunal Interchange about 2.5 million years ago. Eight species of bats with Neotropical affinities are found in the late Pliocene and Pleistocene of Florida, including two species of Mormoopidae, *Mormoops megalophylla* and *Pteronotus* cf. *P. pristinus*; two species of Phyllostomidae, *Desmodus archaeodaptes* and *D. stocki*; three species of Molossidae, *Eumops glaucinus, E. underwoodi,* and *Tadarida brasiliensis*; and one species of Vespertilionidae, a large undescribed species of *Antrozous.* Of these species only *E. glaucinus* and *T. brasiliensis* presently occur in Florida, whereas *M. megalophylla* and *E. underwoodi* are extinct in Florida but survive in tropical America. *P. pristinus,* the vampire bats *Desmodus archaeodaptes* and *D. stocki,* and the large *Antrozous* are extinct species. A ninth Neotropical bat, *Artibeus jamaicensis,* has been reported from the Florida Keys based solely on sight records. The Neotropical bats recorded from the Recent and fossil fauna of Florida were ultimately derived from either Middle America or the West Indies. The bats that originated in Middle America reached Florida from the west by an overland route along the northern Gulf Coast. Antillean bats colonized South Florida by overwater dispersal from Cuba or the Bahamas. Among the nine species of Florida bats with Neotropical affinities, *Pteronotus* cf. *P. pristinus* and *Artibeus jamaicensis* are West Indian in origin; *Desmodus archaeodaptes, D. stocki,* and *Eumops underwoodi* were derived from Middle America; *Eumops glaucinus* could have come from either the West Indies or Middle America; *Tadarida brasiliensis* and *Antrozous* sp. were derived from either Middle America or the western United States; and *Mormoops megalophylla* occurs in all three of these regions. The extinction of most of these tropical bats from Florida can be attributed to either decreased climatic equability or the disappearance of extensive cave systems in the central and southern peninsula.

INTRODUCTION

Although Florida is often portrayed as a subtropical refugium, the mammalian fauna presently inhabiting the state does not exhibit a particularly strong tropical influence. Florida possesses a depauperate fauna of 55 species of land mammals consisting primarily of south temperate species that are widespread throughout the southeastern United States (Brown, 1987). The Florida peninsula has fewer species of mammals than any other region of comparable size in North America south of 50°N latitude (Simpson, 1964). There are, however, four species of land mammals recorded from Florida that do not occur elsewhere in North America north of Mexico. Two of these species are Neotropical bats and two are endemic rodents.

Southern peninsular Florida is the only region in the United States where Wagner's mastiff bat, *Eumops glaucinus,* is found (Koopman, 1971; Belwood, 1981). Otherwise, this Neotropical species occurs from Mexico southward into South America and on Cuba and Jamaica in the West Indies. The Jamaican fruit-eating bat, *Artibeus jamaicensis,* has been reported from the Florida Keys

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on several occasions (Maynard, 1872; Lazell and Koopman, 1985; Lazell, 1989), although others have disputed these records (Allen, 1911; Humphrey and Brown, 1986). *A. jamaicensis* is one of the most widespread of all Neotropical frugivorous bats, but it is unknown elsewhere in the United States. The closest viable population of *A. jamaicensis* occurs in Cuba.

The Florida mouse, *Podomys floridanus,* is endemic to the peninsula and eastern panhandle of Florida. Prior to the work of Carleton, *Podomys* was considered a subgenus of *Peromyscus. Podomys* shares a common ancestor with the genera *Habromys* (also formerly a subgenus of *Peromyscus*) and *Neotomodon* (Carleton, 1980). The single species of *Neotomodon* and the four species of *Habromys* are all found at higher elevations in Middle America (Hall, 1981). The occurrence of its closest sister taxa in Middle America suggests that *Podomys floridanus* probably had its origins in this region as well. The earliest record of *Podomys* is from the early Irvingtonian Haile 21A local fauna in Alachua County in northern peninsular Florida (Morgan et al., 1988). The round-tailed muskrat, *Neofiber alleni,* is endemic to Florida and the Okefenokee Swamp in southernmost Georgia. Unlike *Eumops glaucinus, Artibeus jamaicensis,* and *Podomys floridanus, N. alleni* almost certainly had its origins in temperate North America.

Three other species of Recent land mammals from Florida with Neotropical affinities are widespread in the southeastern United States: the opossum, *Didelphis virginiana*; the nine-banded armadillo, *Dasypus novemcinctus*; and the rice rat, *Oryzomys palustris.* The earliest North American record of *Didelphis virginiana* is from the middle Pleistocene (late Irvingtonian) Coleman 2A fauna in Sumter County, Florida (Martin, 1974). *Dasypus novemcinctus* has invaded Florida naturally from the west within the last 30 years, although this species was introduced into the Florida peninsula in the 1920s (Humphrey, 1974). *Dasypus bellus,* a large extinct relative of *D. novemcinctus,* occurs in many Florida fossil sites between the late Pliocene (late Blancan) and the end of the Pleistocene. *Oryzomys palustris* has been recorded only in late Pleistocene (Rancholabrean) faunas in Florida. The Neotropical sigmodontine rodents had their origins in North America prior to the Great American Interchange in the late Pliocene (Baskin, 1986), but this group, including the oryzomyines, underwent much of its evolutionary radiation in tropical Middle America or South America following the Interchange. A single species of oryzomyine, *O. palustris,* dispersed northward into the southeastern United States in the late Pleistocene.

One extant and one very recently extinct species of marine mammal recorded from Florida are also primarily Neotropical in distribution. The West Indian manatee, *Trichechus manatus,* now occurs in coastal marine habitats and rivers throughout peninsular Florida. The natural range of the West Indian manatee also includes the Greater Antilles, the Gulf and Caribbean coasts of eastern Mexico, the Caribbean coast of Central America, and northern and eastern South America (Lefebvre et al., 1989). *T. manatus* is recorded from scattered fossil sites in Florida from the late Blancan to the late Rancholabrean (Domning, 1982). The West Indian monk seal, *Monachus tropicalis,* has gone extinct only within the last 40 years (Kenyon, 1977). The historical range of this tropical seal was apparently limited to the extreme southernmost portion of the Florida peninsula and the Florida Keys (Allen, 1942; Ray, 1961), as well as the Caribbean Sea and the southern Gulf of Mexico. There are records of *M. tropicalis* from archaeological sites in Florida as far north as Pinellas County on the Gulf Coast and Brevard County on the Atlantic Coast (Ray, 1961; Cumbaa, 1980). *M. tropicalis* is also known from the late Pleistocene (late Rancholabrean) Melbourne local fauna in Brevard County (Ray, 1958). An undetermined species of *Monachus* that may be referable to *M. tropicalis* has been identified in two Florida early Pleistocene (early Irvingtonian) faunas from the southern Gulf Coast: the Leisey Shell Pit in Hillsborough County (Hulbert and Morgan, 1989) and the Rigby Shell Pit in Sarasota County.

The late Pliocene and Pleistocene fossil record provides convincing evidence that at certain times within the past 2.5 million years, Florida supported a much richer fauna of land mammals with Neotropical affinities. There are eight species of bats known from Florida

Plio-Pleistocene fossil sites whose origins were in tropical America, only two of which are still found in the state: the molossids *Tadarida brasiliensis* and *Eumops glaucinus*. Four of the remaining six species are extinct: the vampire bats *Desmodus archaeodaptes* and *D. stocki*, the mormoopid *Pteronotus pristinus*, and a large species of the vespertilionid *Antrozous*. The last two species—the mormoopid *Mormoops megalophylla* and the molossid *Eumops underwoodi*—still inhabit the southwestern United States and Middle America, but no longer occur in Florida.

The discussion of the fossil bats is preceded by a brief zoogeographic review of the Recent Florida chiropteran fauna. The summary of the modern bat fauna is followed by a synopsis of the Pliocene, Pleistocene, and Holocene fossil sites from Florida that contain remains of Neotropical bats and systematic accounts of the individual bat species with tropical affinities. The remainder of the paper considers the various factors that have influenced the zoogeography of Florida's Neotropical chiropteran fauna.

Acknowledgments

I am honored to contribute a paper to a volume dedicated to Dr. Karl F. Koopman. My original impetus to study bats can be traced back to a trip to the AMNH, where Dr. Koopman's help and enthusiastic support for my research on fossil bats from the Cayman Islands led to a lifelong interest in chiropteran systematics, biogeography, and evolution. I thank N. J. Czaplewski, T. A. Griffiths, and A. E. Pratt for reviewing the manuscript and T. A. Griffiths for his patience and dedication in organizing and editing this volume. For permitting study of specimens under their care I am grateful to M. S. Hafner of the Louisiana State University Museum of Zoology, R. M. Timm of the University of Kansas Museum of Natural History, M. D. Carleton and L. K. Gordon of the National Museum of Natural History, and, of course, K. F. Koopman of the American Museum of Natural History. Stephen Beck generously donated fossils of *Eumops underwoodi* and many other species from the Lecanto site to the FLMNH.

ZOOGEOGRAPHY OF FLORIDA'S RECENT BAT FAUNA

Florida is divided into three geographic regions based on the overall distribution of the chiropteran fauna (see divisions marked on map in fig. 1). The exact boundaries between these regions have been arbitrarily drawn to conform to established county lines. These three subdivisions of Florida are hereafter capitalized in the text to distinguish them from other geographic terms: (1) *Panhandle*—from Escambia County in extreme western Florida to Jefferson County in the east. The Aucilla River is the eastern boundary of the Panhandle region, Alabama is the western boundary, and Alabama and Georgia form the northern boundary; (2) *Northern Peninsula*—from Jefferson County on the west and Georgia on the north, south to the northern edge of Lake Okeechobee at about latitude 27° north. The southernmost tier of counties in this region from west to east is Sarasota, De Soto, Highlands, Okeechobee, and St. Lucie; (3) *Southern Peninsula and Keys* (*South Florida* is used interchangeably for this region)—from the northern edge of Lake Okeechobee south to the southern tip of the peninsula and including the Florida Keys. The northernmost tier of counties in this region from west to east is Charlotte, Glades, and Martin. Because these geographic divisions are intended to reflect general patterns in bat species distributions, they are not necessarily equal in size. For example, the region termed the Northern Peninsula actually occupies the northern two-thirds of the Florida peninsula, but reflects the fact that a number of bat species are restricted to the region north of Lake Okeechobee.

Seventeen species of bats have been recorded from the Recent fauna of Florida, including one species of Phyllostomidae, 14 species of Vespertilionidae, and two species of Molossidae (see table 1). Only 11 of these species are known to be breeding residents in Florida, whereas the remaining six species are rare transients or accidentals.

Artibeus jamaicensis is the only member of the Florida bat fauna not represented by a museum specimen collected from the state. This species was first reported from the Florida Keys in the last century by Maynard

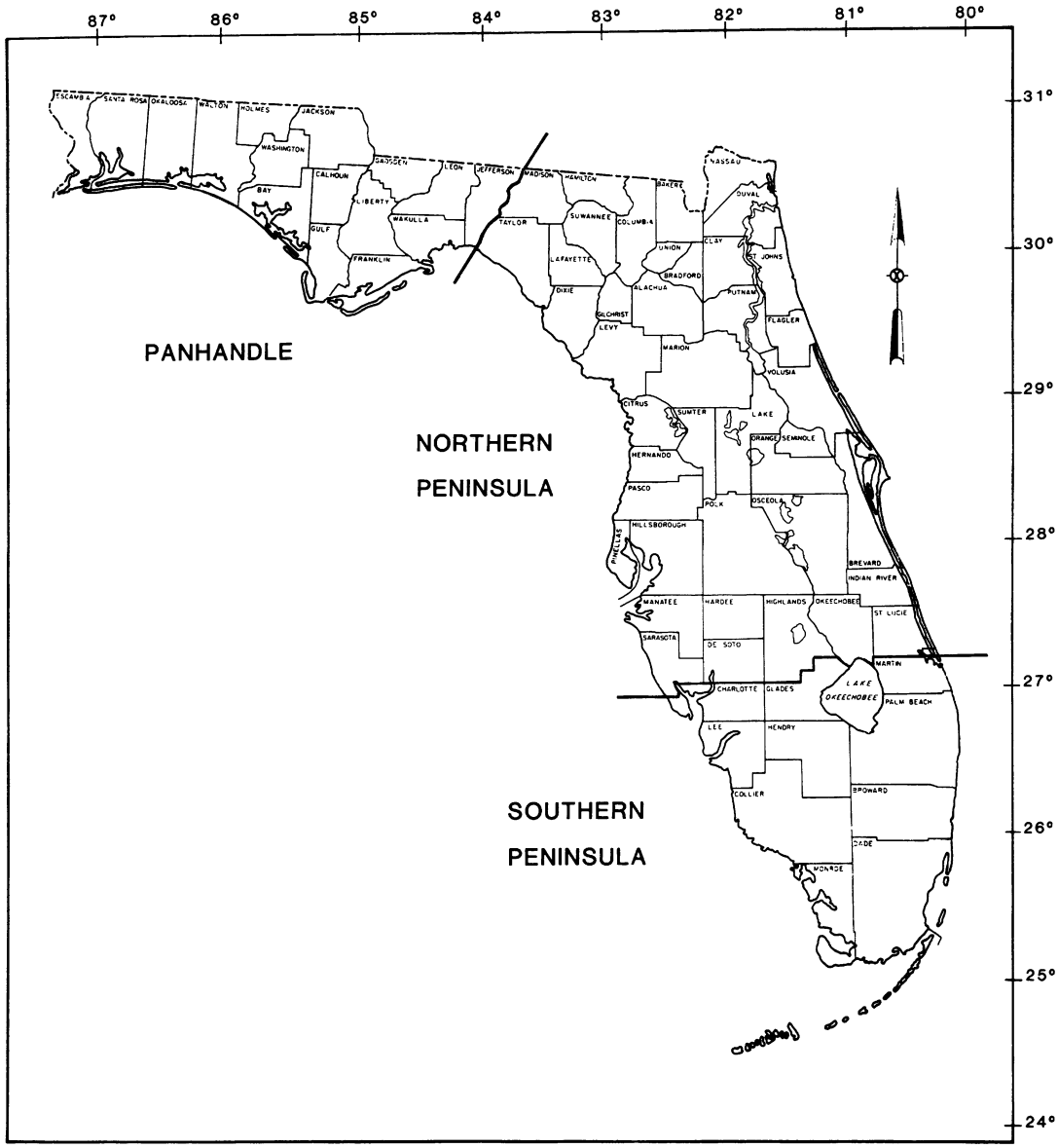

Fig. 1. Map of Florida with county names, showing the three geographic subdivisions of the state recognized in the text based on bat distributions. Heavy black lines mark the boundaries between the three regions.

(1872), who called it *A. perspiccilalune,* an obvious misspelling of *A. perspicillatus,* the commonly accepted name for *A. jamaicensis* at that time. Maynard (1872: 144) noted: "While at Key West in the early winter of 1870, I observed several large bats flying about the city. . . . I was, therefore, agreeably surprised one morning to see a boy enter my room with a bat in his hand, which from its large size I knew could be no other than the species which I had so long desired to obtain. He said that he had found it hanging upon the leaf of a tree. . . . It is a leaf-nosed bat, and Dr. Harrison Allen has kindly identified it, from sketches sent to him. . . ." Harrison Allen, who was the foremost American au-

TABLE 1
Distribution, Zoogeographic Origin, and Status of the Recent Species of Bats Recorded from Florida

Species	Distribution in Florida[a]	Zoogeographic origin[b]	Status[c]
Family Phyllostomidae			
Artibeus jamaicensis	SP	Neotropical (WI)	transient
Family Vespertilionidae			
Myotis austroriparius	P, NP	eastern NA	permanent
M. grisescens	P	eastern NA	permanent
M. keenii	P	temperate NA	transient
M. lucifugus	P	temperate NA	transient
M. sodalis	P	eastern NA	transient
Lasionycteris noctivagans	P	temperate NA	transient
Pipistrellus subflavus	P, NP	eastern NA	permanent
Plecotus rafinesquii	P, NP	eastern NA	permanent
Eptesicus fuscus	P, NP	temperate NA	permanent
Lasiurus borealis	P, NP	temperate NA	permanent
L. cinereus	P, NP	temperate NA	transient
L. intermedius	P, NP, SP	eastern NA	permanent
L. seminolus	P, NP, SP	eastern NA	permanent
Nycticeius humeralis	P, NP, SP	eastern NA	permanent
Family Molossidae			
Tadarida brasiliensis	P, NP, SP	Neotropical (MA)	permanent
Eumops glaucinus	SP	Neotropical	permanent

[a] Florida is divided into three geographic regions on the basis of bat distributions (see fig. 1 and discussion in text). These three regions and their abbreviations are Panhandle (P), Northern Peninsula (NP), and Southern Peninsula and Keys (SP).

[b] Abbreviations are as follows: North America (NA), Middle America (MA), and West Indies (WI). Species listed as temperate NA are widespread throughout much of temperate North America, whereas those species listed as eastern NA have more restricted ranges in the eastern portion of the continent. Among the three Neotropical species, one is derived from the West Indies, one from Middle America, and the other could be from either region.

[c] Status refers to the breeding status of the species in Florida. Permanent species live most of the year in Florida and breed there, whereas transients are very rare in occurrence and are not known to support breeding colonies in the state. The six transient species are all known by fewer than 10 specimens from the state; three species are represented by a single specimen and one (*Artibeus jamaicensis*) is known only from sight records.

thority on bats in the late 19th century, stated (1893: 53, footnote): "Mr. Maynard kindly sent me a drawing of the bat he describes. I have no hesitation in identifying it as *Artibeus perspicillatus.*"

Perhaps because Maynard's specimen was never preserved and no other individuals were collected after 1870, the Key West record of *Artibeus jamaicensis* was generally disregarded by later workers (e.g., G. M. Allen, 1911) until Lazell and Koopman (1985) reported a specimen of *A. jamaicensis* found roosting in a building on Key West in 1983. They published a photograph of this bat, but the specimen was not collected to positively confirm the identification. Humphrey and Brown (1986) disputed Lazell and Koopman's identification of this bat as *A. jamaicensis,* citing several features of the published photograph that suggested to them this bat was some other similar-sized member of the Phyllostomidae. Humphrey and Brown also noted the lack of strong evidence for a resident population of *A. jamaicensis* in the Florida Keys and the highly seasonal climate on these islands, which would presumably limit the availability of fruit during certain times of the year. Lazell (1989) discussed additional sight records of *A. jamaicensis* from Cudjoe Key and Ramrod Key. He also argued that fruit is available throughout the year in the Lower Florida Keys, in particular, native species of the fig, *Ficus.*

Artibeus jamaicensis is a large conspicuous

bat whose presence could hardly go unnoticed by biologists and naturalists if there was indeed a resident breeding population in the Florida Keys. The absence of specimens and the extremely rare sightings of *A. jamaicensis* from the Florida Keys indicate that there is not a permanent population. However, it also seems highly probable that *A. jamaicensis* does occasionally occur in the Florida Keys based on the bat collected at Key West in 1870 (Maynard, 1872), the photograph in Lazell and Koopman (1985), and other sightings discussed by Lazell (1989). The most likely explanation seems to be that on rare occasions individuals of *A. jamaicensis* disperse across the Florida Straits from Cuba, but fail to establish a resident population. Until more convincing evidence is presented that *A. jamaicensis* is a permanent inhabitant of the Florida Keys, the occurrence of this species in Florida should be regarded as accidental, following the usage commonly applied to birds that occasionally wander outside their normal range. At least 21 species of West Indian birds have been reported as accidentals in South Florida (Robertson and Kushlan, 1974).

Four of the six nonresident species of bats recorded from Florida have been found only in the Panhandle, and a fifth species is known to occur in both the Panhandle and the Northern Peninsula. Two of these transient species have been reported from Florida only within the past 10 years. *Myotis lucifugus* is known from a single specimen collected in 1984 in Okaloosa County in the western Panhandle (Brown, 1985), and *Lasionycteris noctivagans* was first recorded from the state based on a specimen taken in 1985 in Santa Rosa County, also in the western Panhandle (Brown, 1986). One specimen of *Myotis keenii* (Rice, 1955b) and two specimens of *Myotis sodalis* (Jennings and Layne, 1957) were obtained in the 1950s from Old Indian Cave in the Florida Caverns State Park near Marianna in Jackson County in the central Panhandle. No individuals of these two species have been found in Florida within the last 20 years. Specimens of *Lasiurus cinereus* have been collected on rare occasions from the Panhandle and as far south as Orange County in the peninsula between October and March. *L. cinereus* appears to migrate through or perhaps overwinter in Florida, but does not have a breeding population in the state.

The remaining 11 species of bats are breeding residents of Florida. Two of these species have very restricted distributions in the state, whereas the other nine species are more widespread. The occurrence of *Myotis grisescens* in Florida is restricted to several breeding colonies from Jackson County in the Panhandle (Rice, 1955a). The only population of *Eumops glaucinus* in the United States occurs in South Florida, with specimens recorded from Charlotte County (Belwood, 1981) on the Gulf Coast and Dade County on the Atlantic Coast (Koopman, 1971; Eger, 1977). Nine species of resident bats occur in the Panhandle and the Northern Peninsula (table 1), whereas only four of these species, along with *E. glaucinus,* are permanent inhabitants of South Florida.

Five species of resident Florida bats occur in the northern two-thirds of the peninsula, but are not found south of Lake Okeechobee. The southernmost limits of these species are between 28 and 27° north latitude in the southern portion of the Northern Peninsula zoogeographic region, which also coincides with the southern terminus of their ranges in eastern North America. For this reason the demarcation between the Northern Peninsula and Southern Peninsula was drawn across the state at about the level of the northern edge of Lake Okeechobee at approximately 27°N (fig. 1). The southernmost confirmed records for these five species are as follows: *Myotis austroriparius,* Bird Key in northwestern Manatee County (Rice, 1957; Jennings, 1958); *Pipistrellus subflavus,* Basinger, Okeechobee County (Davis, 1957; disregarding the questionable sight record from Sugarloaf Key of Hardin, 1975); *Lasiurus borealis,* southeastern Hardee County (Jennings, 1958); *Eptesicus fuscus,* Englewood in southern Sarasota County (Jennings, 1958); *Plecotus rafinesquii,* northwestern Highlands County (Brown, 1974). The absence of *E. fuscus* and *L. borealis* in southern peninsular Florida and the Keys is puzzling because both species occur widely throughout the West Indies and Middle America.

Several authors have suggested that the depauperate Recent bat fauna of South Florida is related in part to the absence of dry caves

in the region (Schwartz, 1952; Layne, 1974; Morgan, 1985). The chiropteran fauna of peninsular Florida south of Lake Okeechobee currently consists of only five species (Layne, 1974): *Lasiurus intermedius, L. seminolus, Nycticeius humeralis, Tadarida brasiliensis,* and *Eumops glaucinus.* None of these five species is known to inhabit caves in Florida. The two species of *Lasiurus* roost almost exclusively in trees, whereas *N. humeralis* roosts in both trees and buildings. *T. brasiliensis* and *E. glaucinus* are found primarily in man-made structures in Florida, although they are known to roost in trees on occasion (Jennings, 1958; Belwood, 1981). All Recent species of bats found in South Florida probably roosted primarily in trees before the extensive construction of buildings during this century.

Three species of bats have been reported from the Florida Keys: *Artibeus jamaicensis, Pipistrellus subflavus,* and *Tadarida brasiliensis* (Lazell and Koopman, 1985). Unfortunately, none of these three species is represented by a museum specimen collected in the Florida Keys. The occurrence of *Artibeus jamaicensis* in the Lower Florida Keys has already been discussed in some detail above. The sight record of *Pipistrellus subflavus* from Sugarloaf Key (Hardin, 1975), if accurate, almost certainly represents a transient individual, because this species is otherwise unknown south of Lake Okeechobee. A specimen of *Tadarida brasiliensis* collected on Bahia Honda in 1979 was subsequently lost (Lazell and Koopman, 1985).

McNab (1974) suggested that the southernmost ranges of many species of north temperate cave-dwelling bats may be limited by their inability to tolerate warm winter temperatures. This is supported by the fact that only 4 of the 15 species of bats recorded from the Florida Panhandle, almost all of which are north temperate species, occur in South Florida. Most species of temperate cave bats that regularly hibernate over winter cannot withstand the high ambient winter temperatures of Florida caves (McNab, 1974). Florida caves are apparently too warm during the winter months to permit hibernation in four of the five species of *Myotis* recorded from the state: *M. grisescens, M. keenii, M. lucifugus,* and *M. sodalis. M. grisescens* maintains breeding colonies in several caves in northern Florida about 20 km south of the Alabama line, but migrates northward to hibernate over winter in cooler caves. Only small nonclustering bats like *Pipistrellus subflavus* are capable of hibernating at environmental temperatures above 14°C (McNab, 1974). *P. subflavus* appears to be the only cave bat that hibernates for an extended period in Florida. The eastern pipistrelle occurs as far south as the southern limit of caves in central Florida. This species would probably be unable to survive much farther south because is appears to have an upper limit for torpor at about 18°C (McNab, 1974). *P. subflavus* is absent from the Rancholabrean Cutler Hammock and Monkey Jungle Hammock cave deposits in South Florida, suggesting that during the late Pleistocene these caves may have had ambient winter temperatures above 18°C.

The warm temperate species *Myotis austroriparius* remains active throughout the year in Florida. The southern limit of *M. austroriparius* in Florida is almost certainly related to the disappearance of caves and not physiological factors. This hypothesis is supported by the presence of *M. austroriparius* in southernmost peninsular Florida during the late Pleistocene in the Monkey Jungle Hammock and Cutler Hammock faunas, both of which appear to have been extensive cave systems.

The decrease in species richness of bats from north to south in the Florida peninsula provides an example of the so-called "peninsula effect" of Simpson (1964). Simpson observed that mammalian species diversity decreased from north to south in Florida and distally on several other North American peninsulas. He attributed this peninsula effect to a higher rate of extinction and lower rate of immigration on peninsulas. The peninsula effect is clearly evident in the distributions of Florida bats listed in table 1. Ten of the 11 resident species of bats in Florida occur in the Panhandle and Northern Peninsula, only five species are definitely recorded from the Southern Peninsula (excluding the Keys), and at most three species inhabit the Florida Keys. The peninsula effect is further magnified by the fact that five of the six nonresident species of bats recorded from

Florida are temperate vespertilionids that reach the southern limits of their ranges in northernmost Florida.

The herpetofauna (Busack and Hedges, 1984; Means and Simberloff, 1987) and avifauna (Cook, 1969; Robertson and Kushlan, 1974) of Florida also exhibit the peninsula effect. Hypotheses to explain the peninsula effect differ among various authors. Busack and Hedges (1984) suggested that historical events are of primary importance in determining species density of snakes and lizards on peninsulas. Means and Simberloff (1987) proposed that the decrease in habitat diversity from north to south in the Florida peninsula explains the decrease in the species diversity of the herpetofauna along this environmental gradient. Cook (1969) and Robertson and Kushlan (1974) favored an historical explanation for the decline in avian species richness as one moves southward in the Florida peninsula. They argued that tropical species of birds in the southern portion of the peninsula were eliminated by past climatic changes and have not been fully replaced, and that the present climate and vegetation of South Florida are not well suited for most north temperate birds.

The reduction in habitat diversity observed in southern peninsular Florida (Means and Simberloff, 1987) appears to have had little effect on bat species richness. The depauperate bat fauna of South Florida has resulted from a combination of factors, including (1) the absence of caves south of the central portion of the peninsula at about 28°N; (2) the inability of many species of temperate bats to adapt to a subtropical environment; and (3) the rarity of tropical bats owing to various barriers to dispersal, including the deep oceanic water gaps between South Florida and the West Indies and the absence of tropical climate and habitats along the Gulf Coast between tropical Mexico and southern Florida.

FLORIDA PLIO-PLEISTOCENE FOSSIL SITES WITH NEOTROPICAL BATS

Bats with Neotropical affinities are known from two late Pliocene faunas, 14 Pleistocene faunas, and three Holocene faunas in Florida. Most of these bat fossils occur in well-known sites. However, three of the local faunas (LF) listed here are as yet unpublished: the late Pleistocene (Rancholabrean) Lecanto 2A LF, Citrus County; the late Rancholabrean Cutler Hammock LF, Dade County; and the Holocene Monkey Jungle 2 LF, Dade County. The brief site descriptions that follow provide the general location, age, and associated chiropteran faunas of all known Florida Plio-Pleistocene localities containing Neotropical bats. A map (fig. 2) shows the location of each of these sites. The numbers of the faunas listed below correspond to the numbers on the map in figure 2. Detailed map data, field notes, and other pertinent information for these localities are on file in the Vertebrate Paleontology collection of the Florida Museum of Natural History (FLMNH, formerly the Florida State Museum).

Many of the following Florida Museum of Natural History vertebrate fossil sites are identified by numbers and letters following the general locality name (e.g., Haile 16A). The name (e.g., Haile) refers to the geographic location of the site, the number identifies the particular quarry or specific area in which the site is located (or was located in some cases), and the letter refers to individual fossil deposits within one quarry or a small localized area. In many previous publications these numbered localities have been referred to by Roman numerals (e.g., Haile XVIA); however, this has led to some confusion, and this practice has been abandoned in favor of Arabic numerals. Ages of sites are given in either millions of years (Ma) or thousands of years (ka).

1. *Macasphalt Shell Pit,* 8 km east of Sarasota, Sarasota County (27°22′N, 82°27′W), late Blancan: Morgan and Ridgway (1987) briefly reviewed the vertebrate fauna from the Macasphalt Shell Pit and provided a list of the land mammals. Hulbert (1988) described a new species of horse, *Cormohipparion emsliei,* from this site. The age of Macasphalt is late Blancan (late Pliocene, between 2.5 and 1.9 Ma) based on the association of *Nannippus phlegon* (= *N. peninsulatus*) with post-Interchange Neotropical immigrants, including the ground sloth *Glossotherium chapadmalense,* the armadillos *Holmesina floridanus* and *Dasypus bellus,* and the cap-

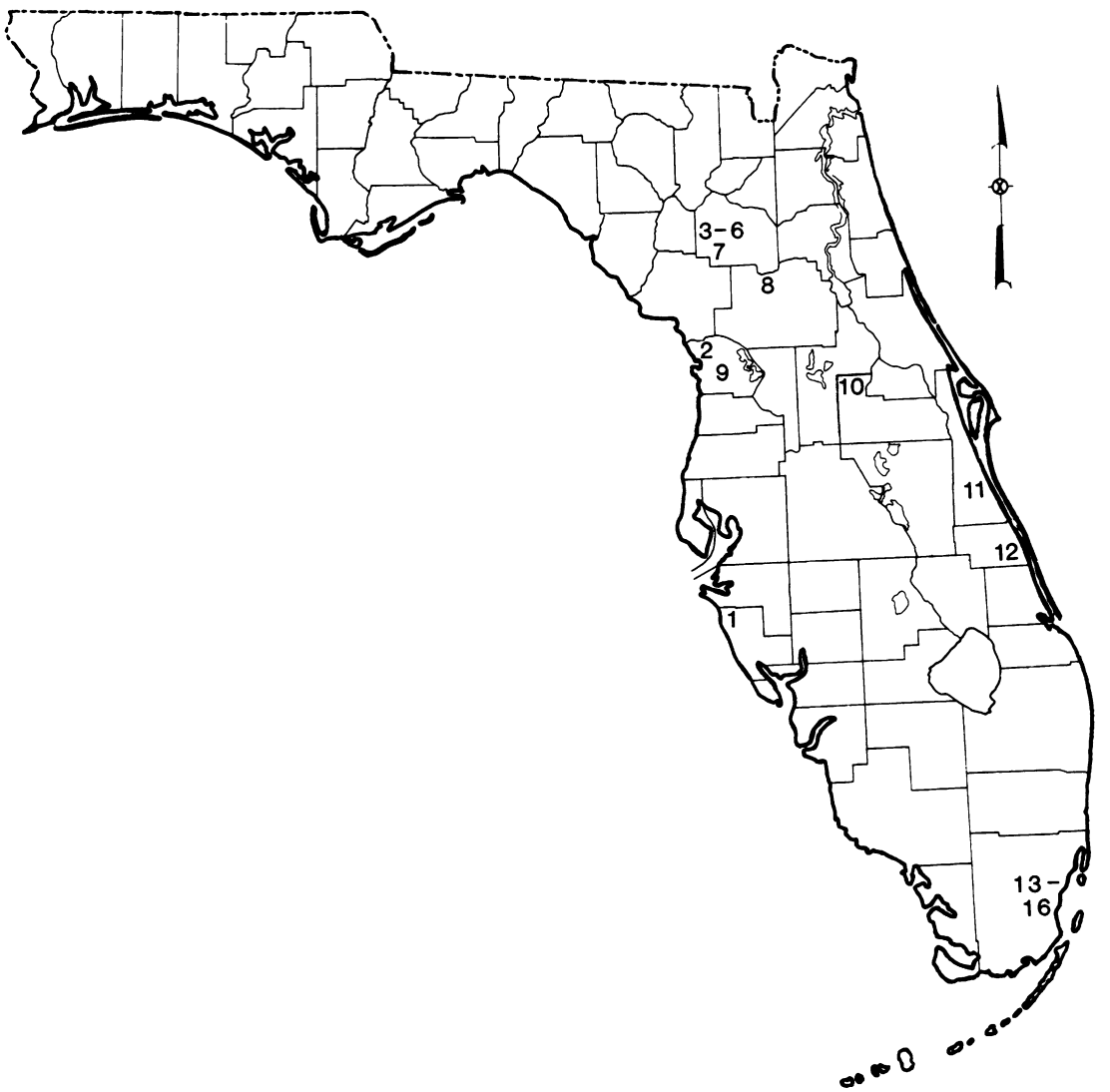

Fig. 2. Map of Florida, showing location of all Pliocene, Pleistocene, and Holocene sites containing fossils of Neotropical bats. **1.** Macasphalt Shell Pit, Sarasota County, late Pliocene (late Blancan). **2.** Inglis 1A, Citrus County, latest Pliocene (earliest Irvingtonian). **3.** Haile 21A, Alachua County, early Pleistocene (early Irvingtonian). **4.** Haile 16A, Alachua County, early Pleistocene (middle Irvingtonian). **5.** Haile 1A, Alachua County, Pleistocene (Irvingtonian/Rancholabrean). **6.** Haile 11B, Alachua County, late Pleistocene (Rancholabrean). **7.** Arredondo 2A, Alachua County, late Pleistocene (Rancholabrean). **8.** Reddick 1A, 1B, 1C, Marion County, late Pleistocene (Rancholabrean). **9.** Lecanto 2A, Citrus County, late Pleistocene (Rancholabrean). **10.** Rock Springs, Orange County, late Pleistocene (Rancholabrean). **11.** Melbourne, Brevard County, latest Pleistocene (late Rancholabrean). **12.** Vero, Indian River County, latest Pleistocene (late Rancholabrean) and Holocene. **13.** Cutler Hammock, Dade County, latest Pleistocene (late Rancholabrean). **14.** Monkey Jungle Hammock, Dade County, latest Pleistocene (late Rancholabrean). **15.** Monkey Jungle 2, Dade County, Holocene. **16.** Nichols Hammock, Dade County, Holocene.

ybara *Neochoerus dichroplax.* A distal humerus of the molossid *Tadarida* sp. is the only bat fossil so far identified from the Macasphalt fauna.

2. *Inglis 1A,* 3 km southwest of Inglis, Citrus County (29°01'N, 82°41'W), earliest Irvingtonian: Webb and Wilkins (1984) provided the most current mammalian faunal list for Inglis 1A. Meylan (1982) described the squamate reptiles from this site, and Carr (1980) reviewed the birds. The Inglis site is very early Irvingtonian in age (between 1.9 and 1.6 Ma). This site is latest Pliocene in age based on the currently recognized time scale (e.g., Berggren et al., 1985), although most previous authors have considered Inglis to be earliest Pleistocene. A number of taxa point to an earliest Irvingtonian age for the Inglis 1A fauna, including several Blancan holdovers such as the glyptodont *Glyptotherium arizonae,* the ground sloth *Megalonyx leptostomus,* the hyaena *Chasmaporthetes ossifragus,* the mustelid *Trigonictis macrodon,* the antilocaprid *Capromeryx arizonensis,* and the phorusrhacid bird *Titanis walleri.* Mammals restricted to the Blancan, such as the canid *Borophagus diversidens* and the horses *Nannippus phlegon* and *Equus* (*Dolichohippus*) are absent from Inglis 1A. A very early Irvingtonian age for this fauna is further indicated by the presence of the rodents *Geomys propinetis* and *Sigmodon curtisi* (Martin, 1979; Wilkins, 1984). Morgan et al. (1988) reported the extinct vampire bat *Desmodus archaeodaptes* from Inglis 1A. Six other species of bats also occur in this fauna, including one species in each of the following six vespertilionid genera: *Antrozous, Eptesicus, Lasiurus, Myotis, Pipistrellus,* and *Plecotus.* With the exception of the vampire, the species-level systematics of the Inglis chiropteran fauna have not yet been resolved, although several new species appear to be present. The Inglis record of *Antrozous* represents the first occurrence of this genus in eastern North America.

3. *Haile 21A,* 5 km northeast of Newberry, Alachua County (29°41'N, 82°35'W), early Irvingtonian: A complete list of the mammals from the Haile 21A locality has not been compiled. Haile 21A is the type locality of the extinct vampire bat *Desmodus archaeodaptes* (Morgan et al., 1988). The site is dominated by a large species of peccary *Platygonus vetus.* The occurrence of the gracile sabrecat *Smilodon gracilis* suggests a pre-late Irvingtonian age for Haile 21A, while the giant tapir *Tapirus haysii* and the association of the canids *Canis edwardii* and *C. armbrusteri* are indicative of late early Irvingtonian faunas in Florida (Hulbert and Morgan, 1989). In addition to *Desmodus archaeodaptes,* Haile 21A has produced a large sample of *Myotis austroriparius.*

4. *Haile 16A,* 6 km northeast of Newberry, Alachua County (29°41'N, 82°34'W), middle Irvingtonian: Many papers have been written on selected mammalian taxa from Haile 16A, but no complete faunal list is available for this site. The extinct cotton rat *Sigmodon libitinus,* described from Haile 16A, is intermediate between *S. curtisi* from the early Irvingtonian Inglis 1A fauna and *S. bakeri* from the late Irvingtonian Coleman 2A fauna (Martin, 1979). A middle Irvingtonian age for Haile 16A is further indicated by the presence of the ground sloth *Megalonyx wheatleyi* (McDonald, 1977) and the arvicoline rodent *Atopomys salvelinus* (Winkler and Grady, 1990) and the stage of evolution of the arvicoline *Pitymys* (R. A. Martin, personal commun.) and the pampathere *Holmesina.* Several postcranial elements of the extinct vampire *Desmodus archaeodaptes* were reported from Haile 16A by Morgan et al. (1988). The small vespertilionid *Myotis austroriparius* is also relatively common in this fauna.

5. *Haile 1A,* 6 km northeast of Newberry, Alachua County (29°41'N, 82°34'W), Irvingtonian/Rancholabrean: Brodkorb (1953) reported on the fossil avifauna from Haile 1A and Auffenberg (1963) described the snakes. Auffenberg (1963) suggested a middle to late Pleistocene age for Haile 1A, but this age assignment cannot be substantiated because the site lacks mammalian biostratigraphic indicators. Gut (1959) referred a single complete humerus from this site to his new species of vampire bat, *Desmodus magnus* (= *D. stocki*).

6. *Haile 11B,* 7 km northeast of Newberry, Alachua County (29°42'N, 82°34'W), Rancholabrean: Ligon (1965) described the extensive avifauna from this site. Large mammals are very rare at Haile 11B, but the

presence of the rodents *Pitymys pinetorum* and *Synaptomys australis* indicates a Rancholabrean age. Hutchison (1967) reported *Desmodus stocki* from Haile 11B. This record was repeated by Ray et al. (1988). The specimens upon which this identification was based cannot now be located. The bats *Pipistrellus subflavus* and *Lasiurus intermedius* also occur at Haile 11B.

7. *Arredondo 2A,* 7 km southwest of Gainesville, Alachua County (29°37'N, 82°24'W), Rancholabrean: A description, map, stratigraphic section, and detailed discussion of the avifauna from Arredondo 2A are given by Brodkorb (1959). Webb and Wilkins (1984) presented a current mammalian faunal list from this site. The age of Arredondo 2A is Rancholabrean based on the occurrence of *Canis dirus, Tapirus veroensis, Bison* sp., *Microtus pennsylvanicus, Pitymys pinetorum,* and *Oryzomys palustris.* The presence of the large extinct vampire *Desmodus stocki* from Arredondo 2A has been noted by many previous workers (Brodkorb, 1959; Hutchison, 1967; Martin, 1972; Webb, 1974; Webb and Wilkins, 1984; Ray et al., 1988). Other bats recorded from Arredondo 2A include *Myotis austroriparius, Eptesicus fuscus,* and *Lasiurus intermedius* (Webb and Wilkins, 1984; Morgan, 1985).

8. *Reddick 1A, 1B, 1C,* 1.3 km southeast of Reddick, Marion County (29°22'N, 82°11'W), Rancholabrean: The Reddick 1 faunas are among the best known and richest Rancholabrean vertebrate assemblages from Florida (Webb, 1974; Kurtén and Anderson, 1980). The three sublocalities in the Reddick 1 Quarry (1A, 1B, 1C) are located within 100 m of one another and may represent portions of a single large cave system. The history of excavations at the Reddick 1 locality, the designations of sublocalities, and a list of the vertebrate fauna are given by Gut and Ray (1963) and Hamon (1964). The age of the Reddick 1 fauna is Rancholabrean based on the presence of *Canis dirus, Tremarctos floridanus, Tapirus veroensis, Bison* sp., *Pitymys pinetorum, Synaptomys australis,* and *Oryzomys palustris.* The tremarctine bear *Tremarctos* occurs in the Irvingtonian and perhaps the Blancan in western North America (Kurtén and Anderson, 1980), but is restricted to the Rancholabrean in Florida. The larger tremarctine *Arctodus pristinus* occurs in Florida Irvingtonian faunas. Reddick 1 is the type locality of *Desmodus magnus* (later synonymized with *D. stocki*) described by Gut (1959). Many authors have noted the presence of *D. stocki* at Reddick 1 (Gut and Ray, 1963; Hutchison, 1967; Martin, 1972; Webb, 1974; Kurtén and Anderson, 1980; Webb and Wilkins, 1984; Morgan et al., 1988; Ray et al., 1988). Vampire bats occur primarily in the Reddick 1B and 1C sublocalities, and are rare at Reddick 1A, the so-called "rodent beds." Other species of bats from Reddick 1 include *Eptesicus fuscus,* a small species of *Lasiurus* (either *L. borealis* or *L. seminolus*), *Lasiurus intermedius, Myotis austroriparius, Pipistrellus subflavus,* and *Tadarida brasiliensis.*

9. *Lecanto 2A,* 2.5 km northwest of Lecanto, Citrus County (28°52'N, 82°30'W), Rancholabrean: A description of the Lecanto 2A LF has not been published previously. The site was excavated in 1985 and 1986 by Stephen Beck, who generously donated a representative sample of the vertebrate fauna to the FLMNH. The Pleistocene vertebrates from Lecanto 2A were preserved in clays and sands that filled a cave or fissure in Eocene marine limestone. The site is rich in large mammals, particularly the camels *Hemiauchenia macrocephala* and *Palaeolama mirifica.* Microvertebrates, including frogs, snakes, birds, shrews, rodents, and bats, are also abundant in certain layers of the Lecanto 2A site. A Rancholabrean age for Lecanto 2A is indicated by the presence of *Canis dirus, Tremarctos floridanus, Tapirus veroensis,* and *Oryzomys palustris.* Two species of bats have been identified from this fauna: *Pipistrellus subflavus* and *Eumops underwoodi.* This represents the first occurrence of the large Neotropical molossid *E. underwoodi* in eastern North America.

10. *Rock Springs,* 10 km north of Apopka, Orange County (28°45'N, 81°30'W), Rancholabrean: Wilkins (1983) reviewed the mammalian fauna from Rock Springs. The presence of *Canis dirus, Tremarctos floridanus, Tapirus veroensis,* and *Bison* sp. are all indicative of Florida Rancholabrean faunas. Although now an underwater artesian spring, Rock Springs was apparently a dry cave system in the late Pleistocene. This suggests that water tables were lower than at the present time and that deposition occurred during a

glacial interval. Wilkins (1983) noted the presence of the pocket gopher *Thomomys orientalis* at Rock Springs. The genus *Thomomys* is typical of more arid habitats in western North America, perhaps another indicator of glacial conditions. Ray et al. (1963) first reported the presence of the Neotropical mormoopid bat *Mormoops megalophylla* in the Rock Springs fauna. Wilkins (1983) further discussed the record of *M. megalophylla* from Rock Springs and added *Myotis austroriparius* to the fauna.

11. *Melbourne,* 5 km west of Melbourne, Brevard County (28°04′N, 80°41′W), late Rancholabrean: The rich mammalian fauna from Melbourne has been reviewed by several authors (Ray, 1958; Webb, 1974; Kurtén and Anderson, 1980). The Melbourne LF occurs above the marine late Pleistocene Anastasia Formation, which dates to the last interglacial (about 125 ka). The Melbourne fauna is considered to be late Rancholabrean in age based on the presence of *Glyptotherium floridanum, Canis dirus, Tremarctos floridanus, Felis concolor, Tapirus veroensis, Bison antiquus, Synaptomys australis,* and *Oryzomys palustris.* The only bat fossil reported from Melbourne is the type specimen of the large molossid *Molossides floridanus* (= *Eumops glaucinus floridanus* after Koopman, 1971) described by Allen (1932).

12. *Vero,* Vero Beach, Indian River County (27°39′N, 80°24′W), late Rancholabrean and Holocene: Discovered early in this century, Vero is one of the best known Rancholabrean faunas from Florida (Weigel, 1962; Webb, 1974; Kurtén and Anderson, 1980; Morgan, 1985). Weigel (1962) reviewed the discovery and excavation of Vero and provided a complete list of the vertebrate fauna, and Webb and Wilkins (1984) updated the mammalian faunal list. Weigel (1962) demonstrated that both late Pleistocene (Stratum 2) and Holocene (Stratum 3) vertebrates are present at Vero. As with the Melbourne fauna, the late Rancholabrean fauna from Vero is located directly above the late Pleistocene (last interglacial) Anastasia Formation. Stratum 2 at Vero contains a number of extinct megafaunal species typical of the Rancholabrean, including *Canis dirus, Tremarctos floridanus, Tapirus veroensis,* and *Bison antiquus.* The fauna from Stratum 3 at Vero is regarded as Holocene in age due to the lack of extinct Pleistocene megafaunal taxa (Weigel, 1962). Morgan (1985) described the rather extensive fossil chiropteran fauna from Vero. Only *Eptesicus fuscus* and *Nycticeius humeralis* are recorded from the late Pleistocene Stratum 2 at Vero, whereas six species of bats occur in the Holocene Stratum 3: *E. fuscus, Lasiurus intermedius, Lasiurus* cf. *L. seminolus, N. humeralis, Tadarida brasiliensis,* and *Eumops glaucinus* (Morgan, 1985).

13. *Cutler Hammock,* 4 km east of Perrine, Dade County (25°37′N, 80°19′W), late Rancholabrean: The extensive Cutler Hammock LF has not yet been published. The Cutler Hammock site was discovered in 1985 and excavated during 1985 and 1986 by personnel from the Historic Preservation Division of Dade County and the FLMNH. The fossils occur in a sinkhole located in a tropical hardwood hammock less than 5 m above sea level and only about 0.3 km inland from the Atlantic Ocean. This sinkhole developed in the oolitic facies of the marine late Pleistocene Miami Limestone. The Miami Limestone was deposited during the last interglacial high sea level stand and has been dated by uranium series at between 140 and 110 ka (Osmond et al., 1965). Therefore, the Cutler Hammock fauna must be younger than the last interglacial and is probably very late Pleistocene (late Rancholabrean, late Wisconsinan) in age, between 20 and 10 ka. Unfortunately, the bones from this site are too highly leached to provide accurate radiocarbon dates (T. W. Stafford, personal commun.). Although still incompletely studied, the Cutler Hammock fauna already exceeds 100 species. To date, 48 species of mammals have been identified from this site, including 16 species of extinct Pleistocene megafauna. A Rancholabrean age for the Cutler Hammock LF is supported by the presence of *Canis dirus, Tremarctos floridanus, Felis concolor, Panthera atrox, Bison antiquus, Pitymys pinetorum,* and *Oryzomys palustris.* Four species of bats have been identified from Cutler Hammock, including the Neotropical mormoopid *Mormoops megalophylla* and the vespertilionids *Eptesicus fuscus, Myotis austroriparius,* and *Nycticeius humeralis.*

14. *Monkey Jungle Hammock,* 5 km west of Goulds, Dade County (25°34′N, 80°26′W), late Rancholabrean: The Monkey Jungle

Hammock LF is located only 12 km southwest of Cutler Hammock. These two sites formed under very similar depositional conditions, are close in age, and have a great number of species in common. The Cutler Hammock and Monkey Jungle Hammock sites are the two southernmost Rancholabrean vertebrate faunas in the continental United States. Monkey Jungle is also located in a sinkhole in a tropical hardwood hammock less than 5 m above sea level. Likewise, the Monkey Jungle Hammock sinkhole formed in the marine late Pleistocene Miami Limestone and is thus younger than 110 ka. Both the Monkey Jungle and Cutler sites seem to have formed during periods of much lower sea level and correspondingly lowered water tables. Consequently, a very late Pleistocene (late Rancholabrean) age is most likely. The Monkey Jungle Hammock LF has been discussed several times (Martin, 1977; Ober, 1978; Morgan, 1985), but no comprehensive vertebrate faunal list is available. Morgan (in press) provided a current mammalian faunal list numbering 43 species, including nine members of the extinct Pleistocene megafauna. Species in the Monkey Jungle Hammock fauna indicative of a Rancholabrean age include *Canis dirus, Tremarctos floridanus, Felis concolor, Panthera atrox, Pitymys pinetorum,* and *Oryzomys palustris.* The chiropteran fauna is composed of eight species: *Mormoops megalophylla* and *Pteronotus* cf. *P. pristinus* (Mormoopidae); *Myotis austroriparius, Eptesicus fuscus,* a small species of *Lasiurus* (either *L. borealis* or *L. seminolus*), and *Nycticeius humeralis* (Vespertilionidae); and *Eumops glaucinus* and *Tadarida brasiliensis* (Molossidae). The two mormoopids and the two molossids have affinities with Neotropica.

15. *Monkey Jungle 2,* 5 km west of Goulds, Dade County (25°34′N, 80°26′W), Holocene: A second sinkhole located within several hundred meters of the original site that produced the Rancholabrean Monkey Jungle Hammock LF was excavated in 1980. This second fauna, here named Monkey Jungle 2, is quite different in age and faunal content from the original Monkey Jungle site. Based on the complete absence of extinct species, Monkey Jungle 2 is Holocene in age. Several postcranial elements of the large molossid *Eumops glaucinus* have been identified from Monkey Jungle 2.

16. *Nichols Hammock,* 1 km northeast of Princeton, Dade County (25°32′N, 80°25′W), Holocene: The vertebrate fauna from the Nichols Hammock site was reviewed by Hirschfeld (1968). This site is also located in a sinkhole in a tropical hardwood hammock that formed in the late Pleistocene Miami Limestone. Nichols Hammock is similar to Monkey Jungle 2, but differs from Cutler Hammock and Monkey Jungle Hammock in the absence of extinct megafauna. It is presumed to be Holocene in age. Hirschfeld (1968) reported *Tadarida brasiliensis* from Nichols Hammock based on a single proximal humerus.

SYSTEMATIC ACCOUNTS

Detailed morphological descriptions, comparisons, and measurements are provided only for those species not previously reported from the Florida fossil record (e.g., *Pteronotus pristinus* and *Eumops underwoodi*) or for species in which the taxonomy is in question (e.g., *Desmodus stocki* and *D. magnus*). Lists of individual specimens with catalogue numbers are not given for most of the species. These data have already been published elsewhere for most of the species, and therefore only the literature citation is given along with a brief description of the material represented (number of specimens and minimum number of individuals [= MNI]). With one exception, all Neotropical bat fossils from Florida are housed in the Vertebrate Paleontology collection of the Florida Museum of Natural History, University of Florida (acronym UF). The one specimen not in the FLMNH collection is the type of *Molossides floridanus,* which belongs to the Museum of Comparative Zoology (MCZ).

FAMILY MORMOOPIDAE SAUSSURE, 1860

Mormoops megalophylla Peters, 1864

FOSSIL RECORD: *Mormoops megalophylla* is known from three late Pleistocene (Rancholabrean) fossil sites in Florida: Rock Springs (Ray et al., 1963; Wilkins, 1983),

Cutler Hammock, and Monkey Jungle Hammock (Morgan, in press). No skulls of *M. megalophylla* are known from Florida, but several mandibles and many postcranial elements are included among the fossils from these three sites. The largest sample of *M. megalophylla* is from Rock Springs (29 specimens, MNI = 6); five specimens (MNI = 2) have been identified from Monkey Jungle and a single proximal humerus is known from the Cutler Hammock site. Late Quaternary fossils of *M. megalophylla* from outside the modern range of the species are also known from the West Indian islands of Cuba, Hispaniola, Jamaica, Andros in the Bahamas, and Tobago (Silva Taboada, 1974; Eshelman and Morgan, 1985; Morgan and Woods, 1986; Morgan, 1989). The disappearance of *M. megalophylla* from the West Indies in the late Pleistocene or early Holocene is difficult to explain because these islands currently support the richest known fauna of Mormoopidae.

MODERN DISTRIBUTION: *Mormoops megalophylla* is primarily a Neotropical species whose range barely extends into the Nearctic Region in southern Texas, Arizona, and northernmost Mexico. This species then occurs southward throughout Mexico to Honduras, but is absent from Nicaragua, Costa Rica, and Panama. *M. megalophylla* is also found in northern South America along the Caribbean coast of Colombia and Venezuela, including the continental islands of Trinidad, Margarita, and the Netherlands Antilles, and in an isolated region of northern Ecuador (Smith, 1972).

DISCUSSION: Ray et al. (1963) first reported *Mormoops megalophylla* from Florida in the Rancholabrean Rock Springs LF. More recently *M. megalophylla* has been identified from the late Rancholabrean Monkey Jungle Hammock and Cutler Hammock faunas, both of which are sinkhole/cave sites in extreme southern peninsular Florida about 350 km south of Rock Springs. *M. megalophylla* is an obligate cave-dwelling bat, and thus it is not surprising that all three of the Florida fossil sites where it has been discovered occur in sinkholes or caves. The extinction of this species in South Florida can probably be attributed to the disappearance of dry caves in the southern half of the peninsula since the end of the Pleistocene. *M. megalophylla* apparently went extinct in South Florida sometime in the very late Pleistocene or early Holocene following the postglacial rise in sea level and flooding of the extensive dry cave systems that occurred in this region during the Wisconsinan glacial interval. Most of the caves presently found in northern and central Florida are very small and may lack a suitable microclimate for *M. megalophylla,* which generally prefers to roost in large caves. In all three Florida Pleistocene faunas in which *M. megalophylla* has been identified, it occurs in association with another cave-dwelling species, *Myotis austroriparius.* Although these two species occurred together in at least three different cave systems in Florida during the late Pleistocene, their modern ranges do not overlap.

Silva Taboada (1974) presented measurements comparing fossils of *Mormoops megalophylla* from two caves in Trinidad, Las Villas Province, Cuba, with fossils of *M. megalophylla* from Rock Springs provided by Ray et al. (1963). Silva Taboada could not distinguish Cuban fossil *M. megalophylla* from the Florida fossils or the Recent mainland form. Proximal width measurements of eight fossil humeri of *M. megalophylla* from the three Florida Pleistocene sites (table 2) are within the observed range of humeri of Recent Neotropical *M. megalophylla,* but are somewhat larger than for a sample of 17 humeri of this species from the Pleistocene of Cuba (Silva Taboada, 1974). However, comparison of the distal width for four humeri of *M. megalophylla* from Florida with one fossil distal humerus each from the Bahamas, Dominican Republic, and Jamaica (measurements of the distal humerus for the Cuban sample are not available) reveals that the Florida and West Indian specimens are virtually identical in size (table 2). No morphological differences could be discerned between the extinct populations of *M. megalophylla* from Florida and the West Indies or between these fossils and modern specimens of *M. megalophylla* from Middle and South America. Therefore, the origin of the Florida *M. megalophylla* cannot be positively established, as they could have been derived from either the West Indies or the mainland Neotropics.

TABLE 2
Measurements (in millimeters) of the Humerus of Recent and Fossil *Mormoops megalophylla*
(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species, age, and locality	Proximal width	Width of distal articular surface	Thickness of shaft
Mormoops megalophylla	3.9	3.2	1.7
Recent	3.8–4.1	3.2–3.3	1.7
Neotropics	4	2	2
M. megalophylla	3.8	3.1	1.7
Fossil	3.7–4.0	3.1–3.2	1.7–1.8
Rock Springs, Florida	5	4	4
M. megalophylla	3.8	—	—
Fossil	3.8	—	—
Monkey Jungle, Florida	2	—	—
M. megalophylla	3.8	—	1.7
Fossil	—	—	—
Cutler Hammock, Florida	1	—	1
M. megalophylla	—	—	—
Fossil	3.5–3.7	—	—
Cuba[a]	17		
M. megalophylla	—	3.1	1.7
Fossil	—	—	—
Andros, Bahamas	—	1	1
M. megalophylla	—	3.1	1.8
Fossil	—	—	—
Dominican Republic	—	1	1
M. megalophylla	—	3.2	1.8
Fossil	—	—	—
Jamaica	—	1	1

[a] Measurements of Cuban fossil *M. megalophylla* are from Silva Taboada (1974), who provided only ranges and not means for his samples.

Pteronotus cf. *P. pristinus* Silva Taboada, 1974

MATERIAL EXAMINED: UF 66501, right mandible with m2–m3; UF 66502, edentulous right mandible with alveoli for c1–p4.

FOSSIL RECORD: Two mandibles of *Pteronotus* cf. *P. pristinus* were identified from the late Pleistocene (late Rancholabrean) Monkey Jungle Hammock LF in southernmost peninsular Florida (Morgan, in press). The only other fossil records of this extinct species are from the type locality—Cueva de los Masones—and from Cueva del Jagüey, both of which are located in Trinidad, Las Villas Province, Cuba (Silva Taboada, 1974, 1979). These two Cuban fossil deposits have not been radiocarbon dated but are certainly Late Quaternary in age.

DISCUSSION: The more complete mandible from Monkey Jungle Hammock (UF 66501) can be distinguished from the mandible of all Recent Florida bats by the greatly reduced coronoid process. Among Neotropical Chiroptera, most species in the Furipteridae, Thyropteridae, Natalidae, and Mormoopidae have a reduced coronoid process. Detailed comparisons with these groups of bats reveal that a close match for the Florida mandible is found only within the mormoopid genus *Pteronotus*. The edentulous anterior portion of a mandible from Monkey Jungle (UF 66502) is also important in the generic determination. One of the most diagnostic dental characters of *Pteronotus* is the presence of a tiny single-rooted, peglike lower p3, wedged between the lingual edges of the considerably larger p2 and p4. In edentulous

TABLE 3

Mandibular and Dental Measurements (in millimeters) of *Pteronotus davyi, P. macleayii,* and *P. pristinus*
(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species, age, and locality	Length of m2–m3	Length of m2	Width of m2	Length of m3	Width of m3	Depth of ramus below m2
Pteronotus davyi	2.82	1.44	0.91	1.45	0.80	1.6
Recent, Mexico	2.76–2.89	1.41–1.48	0.89–0.92	1.41–1.49	0.77–0.83	1.5–1.7
(N = 10)						
P. macleayii	2.82	1.45	0.89	1.46	0.77	1.4
Recent, Cuba	2.76–2.84	1.41–1.49	0.85–0.92	1.42–1.48	0.75–0.78	1.3–1.4
(N = 8)						
P. pristinus	3.0	—	—	—	—	1.5
Fossil, Cuba[a]						
(N = 1)						
Pteronotus cf. *P. pristinus*	3.04	1.57	0.97	1.58	0.84	1.5
Fossil, Florida						
(N = 1)						
(UF 66501)						

[a] Measurements of *P. pristinus* mandible from Cuba taken from photograph in Silva Taboada (1974: pl. 3).

mandibles this dental pattern is revealed by a large alveolus for the single-rooted p2, a very small, rounded, lingually positioned alveolus for the p3, and two large alveoli for the double-rooted p4. This is precisely the arrangement of alveoli in the Monkey Jungle mandible. No living Florida bat has a tiny peglike p3 that is considerably smaller than the p2. Other characters, such as the location and form of the mental foramen and the structure of the mandibular symphysis, confirm the identification of this specimen as *Pteronotus.*

The two Monkey Jungle mandibles were compared to mandibles of all six Recent species of *Pteronotus.* Among these species, *P. parnellii* and *P. gymnonotus* are larger than the fossils, and *P. quadridens* and *P. personatus* are smaller. The Monkey Jungle mandibles are slightly larger than mandibles of *P. davyi* and *P. macleayii* (table 3). The horizontal ramus of the fossil is more slender and has a straighter ventral margin than *P. davyi.* The Florida fossils are most similar in morphology to the Greater Antillean slender-jawed species of *Pteronotus* (subgenus *Chilonycteris*), including *P. macleayii* and *P. quadridens.* Aside from its larger teeth, the slender mandibular ramus of the Monkey Jungle fossil compares most favorably with *P. macleayii.*

Silva Taboada (1974) described *Pteronotus pristinus,* an extinct species from the Late Quaternary of Cuba that is somewhat larger than *P. macleayii* and has a slender mandibular ramus. Although comparative material of *P. pristinus* was not available for study, the two Florida fossils are similar to this species in size and morphology based on the descriptions, measurements, and photographs in Silva Taboada (1974). Measurements taken directly from the photograph of a *P. pristinus* mandible (Silva Taboada, 1974: pl. 3), although admittedly imprecise, are very similar to measurements of the more complete Monkey Jungle mandible (table 3). This identification must be considered tentative until the Monkey Jungle mandibles can be compared directly with *P. pristinus.* Should further comparisons show the Monkey Jungle fossils to be distinct from *P. pristinus,* then they almost surely represent an undescribed species.

No species of *Pteronotus* has been recorded previously from the continental United States, although *P. davyi, P. parnellii,* and *P. personatus* occur in the states of Sonora and Tamaulipas in northern Mexico within several

hundred kilometers of the international boundary. *P. macleayii, P. parnellii,* and *P. quadridens* occur in Cuba less than 150 km south of the Florida Keys. Considering the diversity of the Mormoopidae in Cuba, particularly during the late Pleistocene (when seven species coexisted there [Silva Taboada, 1974]), and the close proximity of that island to Florida and the Florida Keys, it is not entirely unexpected to find a Cuban species of *Pteronotus* in a late Pleistocene fossil site in southern Florida.

Both small Antillean species of the subgenus *Pteronotus* (*Chilonycteris*)—*P. macleayii* and *P. quadridens*—prefer to roost deep within large caves that have a microclimate characterized by high temperature and humidity (Goodwin, 1970; Silva Taboada, 1979). The presence in the late Pleistocene of South Florida of a species of *Pteronotus* closely related to *P. macleayii* and *P. quadridens* adds further support to evidence provided by the occurrence of *Mormoops megalophylla* in two fossil cave deposits in this region—that southernmost peninsular Florida almost certainly possessed extensive cave systems during the late Wisconsinan low sea level stand.

FAMILY PHYLLOSTOMIDAE

SUBFAMILY DESMODONTINAE

Desmodus archaeodaptes
Morgan, Linares, and Ray, 1988

FOSSIL RECORD: The extinct vampire bat *Desmodus archaeodaptes* is known from one latest Pliocene (very early Irvingtonian) and two early to middle Pleistocene (early to middle Irvingtonian) sites in northern peninsular Florida ranging in age from about 1.9 to 0.8 Ma (Morgan et al., 1988). These sites include the earliest Irvingtonian Inglis 1A LF (complete humerus), the early Irvingtonian Haile 21A LF (the type locality; 3 specimens, MNI = 2), and the middle Irvingtonian Haile 16A LF (2 specimens, MNI = 1).

DISCUSSION: Morgan et al. (1988) described the skull of *Desmodus archaeodaptes* and compared it with the large extinct vampire bats *D. stocki* and *D. draculae* and the Recent vampire *D. rotundus*. *D. archaeodaptes* broadly overlaps in size with the living *D. rotundus,* but is smaller than the late Pleistocene species *D. stocki* (table 4) and is much smaller than the giant *D. draculae* from South America (Morgan et al., 1988). *D. archaeodaptes* differs from other species of *Desmodus* in possessing a broad platelike mastoid process, narrower occiput, lateral connection of the nuchal crest to the paroccipital process, nearly vertical orientation of the supraoccipital, lack of inflation and ventral flexion of the posterior portion of the braincase, and posteriorly oriented foramen magnum. *D. archaeodaptes* differs from *D. rotundus* in having a larger glenoid fossa, reduced postglenoid process, smaller occipital protuberance, and weakly inflated suproccipital; and from *D. stocki* in its longer and narrower braincase, weaker cranial crests, ventrally deflected paroccipital process, shallow basicranial pits separated by a low indistinct ridge, and weakly inflated posteromedial process of basisphenoid. See Morgan et al. (1988: fig. 1) for photographs of the type skull of *D. archaeodaptes.*

Several characters present in *Desmodus archaeodaptes* appear to be primitive compared to *D. rotundus*: (1) less expanded or inflated posterior portion of the braincase; (2) more vertical occiput, resulting from the lesser degree of ventral flexion of the braincase; (3) posterior, rather than ventral, orientation of the foramen magnum; and (4) larger glenoid process and smaller postglenoid process, allowing for greater freedom of movement of the lower jaw. The late Pliocene and early Pleistocene species of *Desmodus* was less specialized in characters relating to the expansion and ventral flexion of the braincase. The posterior expansion of the braincase in *D. rotundus* probably reflects the enlargement of certain portions of the brain, particularly the cerebral hemispheres and the vermiform body of the cerebellum (McDaniel, 1976). These two features may be related to the complex motor skills necessary for the unique mode of terrestrial locomotion found only in *D. rotundus* among living bats (Altenbach, 1979). The position in which the head is held during terrestrial locomotion may also have affected the apparent reorientation of the braincase in *D. rotundus* compared to earlier species of *Desmodus.* The more primitive braincase of *D. archaeodaptes* suggests that this species

TABLE 4

Cranial Measurements (in millimeters) of *Desmodus rotundus, D. stocki,* and *D. archaeodaptes*

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Taxon and locality	Total length of skull	Condylobasal length	Breadth of rostrum	Interorbital constriction	Zygomatic breadth	Mastoid breadth	Breadth of braincase	Length of braincase	Height of braincase
Desmodus rotundus	23.7	21.2	6.0	5.5	12.0	12.5	11.9	16.9	11.9
murinus	22.7–24.3	20.5–21.8	5.5–6.5	5.1–5.8	11.5–12.7	12.0–13.1	11.5–12.5	16.4–17.9	11.1–12.6
Mexico (N = 30)									
D. r. rotundus	24.8	22.3	6.6	5.7	12.8	13.0	12.6	17.4	12.3
Chile and Paraguay (N = 10)	24.1–25.5	21.5–23.3	6.1–7.0	5.4–6.0	12.3–13.1	12.6–13.3	12.1–13.0	17.1–18.2	11.9–12.6
D. stocki	27.3	24.5	7.4	6.1	14.0	14.1	13.8	19.2	13.5
San Josecito Cave, Mexico	26.5–28.2	24.1–24.7	7.1–7.6	5.9–6.2	14.0	13.5–14.5	13.6–14.2	18.7–19.7	13.2–13.8
	6	6	6	9	2	8	11	9	10
D. stocki	—	—	—	6.1	14.3	14.4	14.1	19.6	13.2
Reddick 1B, 1C, Florida				5.8–6.3	14.1–14.5	14.1–14.7	13.8–14.4	19.5–19.7	13.0–13.5
				3	2	5	4	3	4
D. archaeodaptes Haile 21A, Florida (N = 1) (UF 94526)	—	—	—	5.8	12.4	12.4	12.3	17.2	12.0

may not have been as highly adapted for terrestrial locomotion as is *D. rotundus.*

Discovery of a species of *Desmodus* in the latest Pliocene and early Pleistocene of Florida in deposits well over a million years older than any previous fossil record of vampire bats adds a new dimension to the evolution and historical biogeography of this intriguing group. Webb (1976, 1985) and Marshall et al. (1979) documented the beginning of the Great American Faunal Interchange in the late Pliocene (late Blancan) around 2.5 Ma ago, shortly after the final closure of the Panamanian isthmus, completing the connection between North and South America. *Desmodus archaeodaptes* or its progenitor probably entered North America in the late Pliocene as a participant in the Great American Interchange, perhaps following the northward dispersal of its principal food source. Koopman (1958) and Morgan and Woods (1986) suggested that during the Late Quaternary, *D. rotundus* from Cuba probably fed upon the small megalonychid ground sloths known from that island, as other suitable "prey" species appear to have been absent. They further hypothesized that the extinction of ground sloths in Cuba led to the disappearance of *D. rotundus* there. Four genera of ground sloths of South American origin are known from Pliocene and Pleistocene deposits in North America, three of which were members of the Interchange fauna.

The large, slow-moving ground sloths or another of the groups of South American immigrant mammals must have originally provided the major source of blood for *Desmodus.* Available evidence suggests that the family Phyllostomidae, which includes the vampire bats of the subfamily Desmodontinae as its most divergent group, evolved in isolation in South America throughout much of the Tertiary. The two most compelling arguments for a South American origin for the Phyllostomidae are that they exhibit a greater range of morphological diversity than any other chiropteran family and that they lack a pre-Interchange fossil record in North America. The only Tertiary fossil records of the Phyllostomidae are the large phyllostomine *Notonycteris magdalenensis* (Savage, 1951) and a second smaller phyllostomine (Czaplewski, 1989), both from the Miocene La Venta fauna of Colombia. Many members of the Phyllostomidae, such as *Desmodus,* now inhabit tropical North America, presumably having dispersed northward from South America following the formation of the Panamanian land bridge in the late Pliocene.

Desmodus stocki Jones, 1958

Desmodus magnus Gut, 1959: 534.

FOSSIL RECORD: The large extinct vampire bat *Desmodus stocki* occurs in four late Pleistocene (Rancholabrean) faunas in northern peninsular Florida (Ray et al., 1988), including the Arredondo 2A LF (16 specimens, MNI = 5), the Haile 1A LF (one complete humerus), Haile 11B LF (specimens not located), and the Reddick 1 fauna (Reddick 1A—9 specimens, MNI = 3; Reddick 1B—153 specimens, MNI = 12; Reddick 1C—179 specimens, MNI = 16). The Haile 1A fauna lacks age-diagnostic taxa of mammals, but is almost certainly Pleistocene, whereas the remaining three faunas are late Pleistocene (Rancholabrean). All occurrences of *D. stocki* from western North America are in late Rancholabrean sites that are located entirely outside the modern range of *D. rotundus* (summarized in Ray et al., 1988). *D. rotundus* now lives farther north on both the Gulf (25°N) and Pacific (28°N) coasts of Mexico than the three Mexican Pleistocene cave sites in which *D. stocki* occurs. However, the fossil localities containing *D. stocki* are all located at elevations above 1000 m on the Mexican Plateau in regions where winter temperatures fall below the 10°C minimum isotherm, which appears to be the primary limiting factor for the distribution of vampire bats (McNab, 1973).

DISCUSSION: One of the first published references to a bat with Neotropical affinities from the Pleistocene of Florida was the description of the large extinct vampire bat *Desmodus magnus* from the Reddick 1 fauna in the north-central region of the peninsula (Gut, 1959). Unfortunately, another species of large late Pleistocene vampire bat, *D. stocki,* was described less than a year earlier from San Josecito Cave, Nuevo Leon, in northern Mexico (Jones, 1958). The papers describing these two new species of large vampires were submitted for publication within 11 days of

one another according to Hutchison (1967), who correctly surmised that neither author was aware of the other's work (H. James Gut, personal commun. to C. E. Ray). To complicate matters, the type series of *D. stocki* (Jones, 1958) included only crania, whereas the type series of *D. magnus* (Gut, 1959) was composed entirely of mandibles. Olsen (1960) described a braincase of *D. magnus* from Reddick, by which time it was known that *D. stocki* antedated *D. magnus*. Without examining specimens of *D. stocki*, Olsen (1960) incorrectly assumed that the braincase of this species closely resembled the braincase of living *D. rotundus*. Thus, he presented only characters to distinguish *D. magnus* from *D. rotundus*, all of which *D. magnus* shares with *D. stocki*. Hutchison (1967) synonymized *D. magnus* with *D. stocki* based on comparisons of the type skull of *D. stocki* with Olsen's descriptions and figures of the braincase of *D. magnus*. Most subsequent authors (Martin, 1972; Kurtén and Anderson, 1980; Morgan et al., 1988; Ray et al., 1988) have followed Hutchison (1967) in regarding *D. magnus* as a junior synonym of *D. stocki*.

Although *Desmodus magnus* and *D. stocki* have been considered conspecific by most recent authors, no one has previously made direct comparisons of the crania of these two species. Furthermore, much additional fossil material of large vampire bats has been collected in the 30 years since these two species were described (see listing in Ray et al., 1988). To determine the taxonomic status of *D. magnus*, I compared five partial crania of this species from Reddick 1 to the type series of 14 crania and partial crania of *D. stocki* from San Josecito Cave. Nine measurements were taken on each of the complete crania of *D. rotundus* and *D. stocki*; at most six measurements could be obtained on the partial skulls from Reddick (table 4). No significant differences were found between *D. magnus* and *D. stocki* in any measurement. Morphological comparisons also revealed no consistent characters that would reliably separate these two forms. Therefore, I agree with Hutchison (1967) and subsequent authors who recognize *D. stocki* as the only valid species of large late Pleistocene vampire bat in North America.

Desmodus stocki is considerably larger than the living Neotropical vampire bat *D. rotundus*. Cranial measurements of *D. stocki* were compared with measurements of 30 crania of Recent *D. rotundus murinus* from the northernmost portion of the species range in northern Mexico (specimens from the states of Nayarit, Nuevo Leon, San Luis Potosí, Tamaulipas, and Veracruz) and 10 crania of *D. r. rotundus* from Chile and Paraguay near the southernmost limit of the species range in southern South America (table 4). There is no overlap in size between the largest Recent specimens of *D. rotundus* and the smallest *D. stocki*, with *D. stocki* averaging 15–20 percent larger in all cranial measurements.

Because the largest individuals of *Desmodus rotundus* occur in temperate latitudes in South America (to about 33°S in Chile and Uruguay), it could be argued that *D. stocki* represents a very large geographic or temporal subspecies of *D. rotundus* that extended its range northward into temperate latitudes during the late Pleistocene. The northernmost occurrence of *D. stocki* is Potter Creek Cave, Shasta County, California, at 40°47′N (Hutchison, 1967). However, the significantly larger size of *D. stocki* compared to the geographically closest population of *D. rotundus* in northern Mexico seems to argue against recognition of *D. stocki* as a large northern subspecies of *D. rotundus*, as there is usually broad overlap in size between two geographically contiguous subspecies. Larger size alone may not be sufficient for species recognition, but there are also important morphological characters unrelated to size that separate *D. stocki* from *D. rotundus*.

Desmodus stocki has a robust skull, and its braincase is larger overall and relatively shorter, broader, and more globose than that of *D. archaeodaptes* or *D. rotundus* (see comparative photographs of the skulls of these three species in Morgan et al., 1988: fig. 1). As a consequence of its larger size, all cranial crests, including the sagittal crest, temporal crests, and nuchal crests, are invariably present and better developed in *D. stocki* than in the smaller *D. rotundus* and *D. archaeodaptes*. The nasal opening and internal choanae of *D. stocki* are relatively broader than in *D. rotundus*. The palate of the larger species is broader, especially posteriorly, whereas the palate of *D. rotundus* is narrower and more concave medially. Only one specimen

TABLE 5

Measurements (in millimeters) of the Humerus of the Recent Vampire Bat *Desmodus rotundus* and the Fossil Species *D. stocki*

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species and locality	Total length	Proximal width	Distal width	Thickness of shaft
Desmodus rotundus	37.0	4.9	5.4	2.1
Neotropics	32.4–42.4	4.4–5.6	4.8	5.9
	19	19	19	19
D. stocki	43.6	6.3	6.8	2.5
San Josecito Cave, Mexico	39.3–47.5	5.8–6.8	6.4–7.3	2.0–2.9
	42	47	52	2
D. stocki	41.8	6.3	6.8	2.6
Reddick 1, Florida (this study)	39.4–44.3	6.0–6.7	6.4–7.2	2.2–2.7
	15	38	42	42
D. stocki	41.1	6.4	6.7	2.7
Reddick 1, Florida (from Gut, 1959)[a]	38.5–43.5	6.1–6.9	6.3–7.3	2.4–2.9
	21	46	66	49

[a] The two samples of *D. stocki* humeri from Reddick 1 are mutually exclusive. The measurements taken from Gut's (1959) original paper describing *D. magnus* are based on a completely different series of specimens than those listed as "this study."

of *D. stocki* has the zygomatic arches complete, although several additional crania from San Josecito and Reddick retain portions of the maxillary or squamosal branches of the zygoma. These specimens indicate that *D. stocki* possessed a thin, delicate zygomatic arch that is not only relatively, but absolutely, more slender than in *D. rotundus,* especially the maxillary portion. The articular surface of the glenoid fossa is comparatively larger in *D. stocki* than in *D. rotundus,* particularly medially. The postglenoid process is relatively smaller in *D. stocki,* being broader, rounder, and shorter than in *D. rotundus,* in which the more prominent postglenoid process is elongated and more sharply triangular in shape. The smaller postglenoid process of *D. stocki,* coupled with the larger articular surface for the mandible, suggests that this species may have had somewhat greater freedom of movement of the lower jaw. There is a thin ridge of bone along the midline bisecting the basisphenoid in both *D. rotundus* and *D. stocki.* This ridge terminates posteriorly as a noticeable swelling in *D. stocki* at about the point of fusion between the basisphenoid and basioccipital, whereas this swelling is weakly developed or absent in *D. rotundus. D. stocki* also possesses two deep pits immediately dorsal and posterior to this swelling on either side of the midline and anteromedial to the tympanic cavities. These pits are weak to absent in *D. rotundus.* The entire pterygoid region in *D. stocki* appears to be flexed more ventrally than in *D. rotundus,* especially anteriorly. In lateral view, the posterior tip of the paroccipital process is posteriorly oriented in *D. stocki,* but is ventrally deflected in *D. rotundus.*

As noted by both Jones (1958) and Gut (1959), the cheek teeth of *Desmodus stocki* are larger and broader than those of *D. rotundus.* The upper incisor of *D. stocki* is less concave on the cutting or posterior surface than in *D. rotundus* (see Jones, 1958: 393, figs. 3, 4), a character also evident in the sample of seven isolated upper incisors of *D. stocki* from Reddick 1. In lateral view, the incisors of *D. stocki* are more procumbent than those of *D. rotundus,* a feature reminiscent of the huge extinct vampire *D. draculae* from Venezuela (see Morgan et al., 1988). The mandible of *D. stocki* is very similar in morphology to that of *D. rotundus,* differing primarily in its larger overall size and more robust cheek teeth.

The primary long bones of the wing—the humerus and radius—average longer and more robust in *Desmodus stocki* than in *D. rotundus* (tables 5, 6). However, the most significant postcranial differences between these two species of vampire bats are in the pro-

TABLE 6

Measurements (in millimeters) of the Radius of the Recent Neotropical Vampire Bat *Desmodus rotundus* and the Fossil Species *D. stocki* from the Reddick 1 Fauna, Florida

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species	Total length	Proximal width	Distal width	Thickness of shaft
Desmodus rotundus	58.0	3.7	3.6	2.5
	54.3–65.5	3.3–4.3	3.3–4.1	2.1–2.9
	15	15	15	15
D. stocki (this study)	65.3	4.5	4.4	2.9
	64.0–66.6	4.3–4.7	4.2–4.6	2.7–3.1
	2	22	9	10
D. stocki (from Gut, 1959)[a]	62.5	4.6	4.5	2.9
	58.8–65.7	4.2–4.9	4.1–5.2	2.5–3.7
	3	45	28	17

[a] See footnote, table 5.

portions of the hind limb. Measurements of the length of the femur and tibia of *D. stocki* from Reddick 1 (tables 7, 8) are approximately equal to or are slightly less than in *D. rotundus*; however, the proximal and distal ends of these two bones, as well as their shafts, are noticeably broader in *D. stocki*. The shaft of the femur is much more massive in *D. stocki* (averaging 30% broader), especially the proximal half. The tibiae of *D. stocki* from Reddick actually average slightly shorter than a sample of 16 tibiae of *D. rotundus*, but the shaft of the fossils averages almost 40% broader and the width of the proximal end is 20% larger. The differences between the femur and tibia of *D. stocki* and *D. rotundus* are striking and certainly not indicative of forms that are conspecific.

Desmodus rotundus has a very robust femur and tibia compared to other bats. The even more robust hind limbs of *D. stocki* suggest the possibility of a somewhat different mode of locomotion than in *D. rotundus*, perhaps related to their larger size or selection of different "prey" species. The larger, more procumbent upper incisors and greater mobility of the larger jaw of *D. stocki* may also reflect differences in prey. The locomotor morphology of *D. rotundus* has been analyzed in detail by Altenbach (1979). A more thorough study of the postcranial elements of the large extinct vampires, including both *D. stocki* and *D. draculae*, may provide important insights into the evolution of the unique terrestrial locomotion of *D. rotundus*.

The occurrence and distribution of fossil vampire bats in Florida has been used as an indicator of interglacial periods, primarily the Sangamonian or last interglacial, and climatic conditions that were warmer than present. No fossil site from Florida containing *Desmodus stocki* has yet been precisely dated, although attempts are now being made to radiocarbon date Rancholabrean cave and fissure deposits in northern peninsular Florida. The two Florida sites with the largest samples of *D. stocki*, Arredondo 2A and Reddick 1, have generally been regarded as Sangamonian in age (e.g., Webb, 1974), due at least in part to the presence of vampire bats. In contrast, all *D. stocki* records from western North America are in Wisconsinan sites (Ray et al., 1988), an apparent contradiction to the Florida records of large vampires. However, when absolute dates become available for Reddick 1, Arredondo 2A, and the other Florida sites containing *D. stocki*, it would not be at all surprising if they prove to be latest Pleistocene (Wisconsinan) in age as well.

McNab (1973) convincingly demonstrated that the living species, *Desmodus rotundus*, is very susceptible to cold temperatures. The northernmost occurrence of this vampire bat is limited by minimum winter temperatures, specifically the 10°C winter isotherm. The southern half of Florida is actually below the 10°C winter isotherm, but this region is isolated from similar climatic regimes in Mexico by a large area with inhospitable climate (at least for vampires) along the northern rim of the Gulf of Mexico. It is reasonable to assume that *D. stocki*, like living vampire bats, did

TABLE 7

Measurements (in millimeters) of the Femur of the Recent Neotropical Vampire Bat *Desmodus rotundus* and the Fossil Species *D. stocki* from the Reddick 1 Fauna, Florida

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species	Total length	Proximal width	Distal width	Thickness of shaft
Desmodus rotundus	24.3	3.7	3.2	2.2
	23.1–26.3	3.3–4.1	2.9–3.6	1.9–2.6
	16	16	16	16
D. stocki (this study)	24.6	4.5	3.8	3.2
	23.3–25.3	4.2–4.8	3.6–4.0	3.0–3.4
	9	24	13	13
D. stocki (from Gut, 1959)[a]	24.5	4.6	3.7	3.4
	23.6–25.5	4.3–4.8	3.5–3.9	3.2–3.7
	7	12	11	8

[a] See footnote, table 5.

not migrate or hibernate. Therefore, the occurrence of *D. stocki* in areas north of the present range of *D. rotundus* indicates one of two things: (1) the large extinct vampire bat was able to withstand somewhat cooler winter temperatures than Recent vampires or (2) climatic conditions were different, specifically winter temperatures were warmer in the late Pleistocene. The larger size of *D. stocki* may have afforded it an advantage in heat conservation over *D. rotundus*. Recent studies indicate that Pleistocene climates in temperate North America, particularly during the latest Pleistocene Wisconsinan glacial interval, were more equable than at present, with warmer winters and cooler summers (Graham and Lundelius, 1984). *D. stocki* may have been well suited to climatic conditions in the warm temperate region of the United States, which were by no means tropical, but lacked the prolonged winter freezes characteristic of the present climate of this region.

FAMILY VESPERTILIONIDAE GRAY, 1821

Antrozous sp.

MATERIAL EXAMINED: UF 124126, right distal humerus.

FOSSIL RECORD: The single partial humerus described here is from the earliest Irvingtonian Inglis 1A LF. This represents the first evidence of *Antrozous* in eastern North America and the third oldest record of the genus. There are two Blancan records of the living species *Antrozous pallidus*: a mandible

TABLE 8

Measurements (in millimeters) of the Tibia of the Recent Neotropical Vampire Bat *Desmodus rotundus* and the Fossil Species *D. stocki* from the Reddick 1 Fauna, Florida

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species	Total length	Proximal width	Distal width	Thickness of shaft
Desmodus rotundus	24.4	2.8	1.6	1.6
	22.7–26.6	2.6–3.0	1.5–1.7	1.5–1.9
	16	16	16	16
D. stocki (this study)	23.5	3.3	1.9	2.4
	23.3–23.6	3.1–3.5	1.9–2.1	2.3–2.5
	4	16	4	14
D. stocki (from Gut, 1959)[a]	23.2	3.4	2.0	2.6
	22.3–24.3	3.3–3.5	1.8–2.0	2.4–2.8
	3	4	4	3

[a] See footnote, table 5.

from the early Blancan (about 3.5 Ma) Beck Ranch LF, Texas (Dalquest, 1978) and a mandible from the middle Blancan (about 3 Ma) Sand Point LF, Idaho (Thewissen and Smith, 1987). All other fossils of *A. pallidus* are from Rancholabrean faunas in the western United States: McKittrick, Potter Creek Cave, and Newport Bay Mesa, all three in California; Isleta Cave, New Mexico; and Papago Springs Cave, Arizona (Kurtén and Anderson, 1980). *A. koopmani* has been reported from five Late Quaternary fossil deposits in Cuba (Silva Taboada, 1979).

DISCUSSION: The distal humerus from the Inglis 1A LF is clearly referable to the living vespertilionid genus *Antrozous*. The Inglis specimen shares the following characteristic features of the distal humerus with *Antrozous*: large, broad medial process with a small distal spinous process; distal portion of the shaft that is broad and somewhat flattened; and deep, well-developed trochlea and central surface of capitulum that are very weakly separated. There are three living species of *Antrozous*—*A. dubiaquercus, A. koopmani,* and *A. pallidus*—although some authors place *A. dubiaquercus* in the monotypic genus *Bauerus* (Engstrom and Wilson, 1981; Engstrom et al., 1987). These three species are all approximately the same size (Silva Taboada, 1979; Hall, 1981). The distal humerus of *Antrozous* from Inglis is about 20% larger than that of *A. pallidus,* and thus in all likelihood represents an undescribed species. Except for its larger size, the Inglis humerus is essentially identical in morphology to that of *A. pallidus.* The fossil compares rather closely in size (but not in morphological characters) to the humerus of *Lasiurus cinereus,* the largest living North American vespertilionid.

Antrozous pallidus is principally an inhabitant of temperate latitudes in the arid regions of western North America, occurring as far east as central Texas. This species does occur south to about 21°N in central Mexico. The other two species of *Antrozous* are both Neotropical in distribution. *A. koopmani* is restricted to Cuba (Silva, 1979), and *A. dubiaquercus* is found from central Mexico south to Costa Rica (Engstrom et al., 1987). The species of *Antrozous* in the Inglis fauna almost certainly reached Florida from the west, but it is unclear whether its origins were in western North America or the Neotropics.

FAMILY MOLOSSIDAE GILL, 1872

Tadarida brasiliensis (I. Geoffroy St.-Hilaire, 1824)

FOSSIL RECORD: *Tadarida brasiliensis* has been identified from four fossil sites in Florida (Morgan, 1985, in press): the Rancholabrean Reddick 1A LF, the late Rancholabrean Monkey Jungle Hammock LF, the Holocene stratum 3 at Vero, and the Holocene Nichol's Hammock fauna. Morgan and Ridgway (1987) identified a distal humerus of *Tadarida,* very similar to if not conspecific with *T. brasiliensis,* from the late Pliocene (late Blancan) Macasphalt Shell Pit fauna in southwestern Florida. Dalquest (1975) reported *Tadarida* sp. from the late Blancan Blanco LF in western Texas. *Tadarida* is rare in all of the fossil localities from Florida in which it has been found (represented by fewer than 10 specimens), suggesting that it probably did not roost in large numbers in Florida caves during the Pleistocene. *T. brasiliensis* has an extensive Late Quaternary fossil record in the West Indies and has also been recorded from Rancholabrean deposits at Mammoth Cave, Kentucky, and Papago Springs Cave, Arizona (Martin, 1972; Kurtén and Anderson, 1980). With the exception of Mammoth Cave, the fossil records are within the modern range of *T. brasiliensis.*

MODERN DISTRIBUTION: *Tadarida brasiliensis* is one of the most widespread bats in the New World, occurring from the southern United States south throughout Middle America, the West Indies, and much of South America south to central Argentina and Chile.

DISCUSSION: Fossils of *Tadarida brasiliensis* from Florida sites compare closely in size with Recent *T. brasiliensis* from the state. This species is common throughout Florida and is the most abundant bat south of Lake Okeechobee (Layne, 1974). *T. brasiliensis* roosts almost exclusively in man-made structures in Florida, although prior to this century probably lived in trees. According to Jennings (1958), *T. brasiliensis* is not known to roost in caves in the southeastern United

States, in marked contrast to the Southwest, where this species inhabits caves in huge numbers.

Tadarida brasiliensis occurs throughout the Greater Antilles and Bahamas, but the various West Indian subspecies are smaller than the Florida race, which is more closely related to *T. brasiliensis* from the southwestern United States and Mexico. One of the earliest records of *Tadarida* in North America is from the late Blancan Macasphalt Shell Pit LF in Sarasota County along the southwestern Gulf Coast (Morgan and Ridgway, 1987). It appears likely that *T. brasiliensis* dispersed from South America to Florida by way of Middle America as an early participant in the Great American Interchange.

Eumops glaucinus floridanus (Allen, 1932)

Molossides floridanus Allen, 1932: 257.
Eumops floridanus: Ray et al., 1963: 377.
Eumops glaucinus floridanus: Koopman, 1971: 4.

FOSSIL RECORD: *Eumops glaucinus* has been identified from four late Pleistocene and Holocene fossil sites in the southern half of the Florida peninsula. Allen (1932) described the holotype mandible of *Molossides floridanus* (= *Eumops glaucinus floridanus* after Ray et al., 1963, and Koopman, 1971) from the late Rancholabrean Melbourne LF located just south of Cape Canaveral along the Atlantic Coast. Martin (1977) described and figured a mandible of *E. glaucinus* from the late Rancholabrean Monkey Jungle Hammock LF, and Morgan (in press) referred several more specimens from Monkey Jungle to this species (4 specimens, MNI = 2). The largest fossil sample of *E. glaucinus* from Florida (9 specimens, MNI = 2) was reported from the Holocene stratum at Vero (Morgan, 1985). The Holocene Monkey Jungle 2 site has yielded a proximal radius of *E. glaucinus* (Morgan, in press). Arroyo-Cabrales and Alvarez (in press) recorded *E. glaucinus* from the caverns at Loltun, Yucatan, Mexico.

MODERN DISTRIBUTION: *Eumops glaucinus* has one of the most restricted ranges of any Recent bat in the United States, where it is known only from Charlotte and Dade counties in southern Florida (Koopman, 1971; Belwood, 1981). *E. glaucinus* was discovered in Charlotte County only within the past 10 years, suggesting that the modern range of this species in Florida may not yet be fully documented (Belwood, 1981). This species also occurs in the Neotropics from central Mexico southward through Central America and much of tropical South America to southern Brazil and Paraguay, and on Cuba and Jamaica in the West Indies. The northernmost modern records of *E. glaucinus* are from Punta Gorda, Charlotte County, Florida (27°N); the vicinity of Miami, Dade County, Florida (26°N); Havana, Cuba (23°N); and Merida, Yucatan, Mexico (21°N). *E. glaucinus* has a widely disjunct distribution because it is not known to occur on the North American continent between southern Florida and central Mexico.

DISCUSSION: Ray et al. (1963) synonymized the extinct genus *Molossides* (Allen, 1932) from the Rancholabrean Melbourne LF with *Eumops*. Koopman (1971) not only recognized *Molossides* (= *Eumops*) *floridanus* as an endemic Florida subspecies of the Recent Neotropical species *E. glaucinus,* but he also established that this bat was still extant in the Miami area. Both Koopman (1971) and Eger (1977) provided measurements demonstrating that Recent specimens of *Eumops glaucinus floridanus* are larger than any other population of *E. glaucinus*. Fossil mandibles of *E. glaucinus* from Melbourne, Monkey Jungle, and Vero are within the size range of Recent mandibles of *E. glaucinus floridanus* from Florida (table 9). All fossils of *E. glaucinus* from Florida are here referred to the endemic subspecies *floridanus* based on their large size. Neotropical representatives of *E. glaucinus* have all been referred to the nominal subspecies, while only the Florida population is sufficiently distinct to warrant a different subspecies designation (Eger, 1977).

The fossil record establishes that *Eumops glaucinus* has inhabited Florida since at least the late Pleistocene. Because the Antillean and mainland Neotropical populations of this species cannot be distinguished, it is not possible to determine the exact origin of the endemic Florida subspecies of *E. glaucinus*. Two biogeographic scenarios are equally plausible for the presence of *E. glaucinus* in Florida. The first hypothesis is that *E. glaucinus* entered Florida from the west at a time when

TABLE 9

Mandibular and Dental Measurements (in millimeters) of *Eumops glaucinus, E. perotis,* and *E. underwoodi*

(Mean, observed range, and sample size, respectively, are provided for each measurement)

Species, age, and locality	Length of m1	Width of m1	Length of m2	Width of m2	Length of m1–m3	Alveolar length of mandibular toothrow	Depth of ramus below m1	Depth of ramus behind m3
Eumops glaucinus	2.7	1.8	2.7	1.7	7.3	11.0	2.4	3.2
Recent	2.6–2.8	1.7–1.8	2.6–2.7	1.7–1.8	7.2–7.5	10.7–11.2	2.3–2.5	3.1–3.3
Florida	7	7	7	7	7	7	3	3
E. glaucinus	2.7	1.8	2.7	1.7	—	—	2.5	—
Fossil								
Vero UF/FGS 7221								
E. glaucinus	2.7	1.8	2.6	1.7	7.3	10.8	2.9	3.4
Fossil								
Monkey Jungle								
UF 20879								
E. glaucinus	2.7	—	2.6	—	7.3	—	—	—
Fossil								
Melbourne								
MCZ 17672[a]								
E. perotis	3.0	2.0	2.9	1.9	8.1	12.8	2.4	3.1
Recent	2.9–3.1	1.9–2.1	2.8–3.0	1.8–2.0	7.9–8.3	12.5–13.2	2.2–2.6	2.9–3.2
	6	6	6	6	6	6	6	6
E. underwoodi	3.1	2.2	3.1	2.0	8.4	12.9	3.0	4.0
Recent	3.1–3.2	2.0–2.3	3.0–3.3	1.9–2.1	8.0–8.7	12.5–13.7	2.7–3.8	3.6–4.6
	10	10	10	10	10	10	10	10
E. underwoodi								
Fossil								
Lecanto 2A								
UF 118437	3.3	2.3	3.2	2.1	8.8	13.6	3.4	4.2
UF 118436	—	—	—	—	—	13.2	3.3	4.2

[a] The mandible of *E. glaucinus* from the Rancholabrean Melbourne local fauna is the type specimen of *Molossides floridanus* Allen (1932).

a number of continental Neotropical mammals extended their ranges northeastward around the Gulf Coast of Mexico to Florida (Webb and Wilkins, 1984; Morgan, 1985). The overland distance between the closest living populations of *E. glaucinus* in central Mexico and southern Florida is approximately 3000 km. The second possibility is that the South Florida population of *E. glaucinus* was derived from the West Indies, specifically Cuba. The closest populations of *E. glaucinus* in Florida and Cuba are now separated by about 300 km; however, this distance would have been reduced to as little as 100 km during low sea level stands in the Pleistocene. Both a Cuban origin and a mainland Neotropical origin for the endemic Florida form of *E. glaucinus* have been postulated (Layne, 1974; Baker and Genoways, 1978; Morgan, 1985).

Eumops underwoodi Goodwin, 1940

MATERIAL EXAMINED: UF 118437, right mandible with c1–m3; UF 118436, edentulous right mandible.

FOSSIL RECORD: Two mandibles of *Eumops underwoodi* are reported from the late Pleistocene (Rancholabrean) Lecanto 2A LF. These specimens represent the first fossil record of this species from the United States and

the only occurrence of *E. underwoodi* in eastern North America. *E. underwoodi* has been reported as a fossil twice previously; from Quaternary strata in Cenote Sagrado at Chichén-Itzá, Yucatan, Mexico (Alvarez, 1976), and from the caverns at Loltún, also from Yucatan (Arroyo-Cabrales and Alvarez, in press). Both Mexican fossil sites are located within the modern range of *E. underwoodi.*

RECENT DISTRIBUTION: *Eumops underwoodi* occurs in Middle America and the southwestern United States, from Nicaragua (about 12°N) north to Arizona (33°N). The smaller of the two subspecies, *E. underwoodi sonoriensis,* occurs in the northwestern portion of the range in Sonora, Mexico, and Arizona, whereas the larger *E. u. underwoodi* inhabits more tropical regions from Mexico south to Honduras and Nicaragua (Eger, 1977; Dolan and Carter, 1979).

DISCUSSION: Preliminary comparisons and measurements reveal that the two fossil mandibles from Lecanto 2A are much too large to be referred to *E. glaucinus,* the only species of *Eumops* currently found in the state (table 9). These two mandibles were compared to mandibles of the largest species of *Eumops* from the western United States and tropical America, including *E. dabbenei, E. perotis, E. trumbulli,* and *E. underwoodi.* Comparisons are made primarily with *E. perotis* and *E. underwoodi,* as these two species both occur in the southwestern United States and Middle America, whereas *E. dabbenei* and *E. trumbulli* are restricted to South America. In characters of the mandible and lower dentition, *E. dabbenei* is very similar to *E. underwoodi,* only much larger, and *E. trumbulli* closely resembles *E. perotis.*

The two fossil mandibles from Lecanto 2A are similar to *Eumops underwoodi* and differ from *E. perotis* primarily in having a much deeper and more massive horizontal ramus (table 9). *E. perotis* has a more elongated, slender dentary. Even though *E. underwoodi* has slightly larger molars (table 9) than *E. perotis,* the mandibular toothrows in the two species are similar in length because *E. perotis* has more widely spaced premolars. The mandibles of the Florida fossil and *E. underwoodi* are noticeably shorter than *E. perotis* between the canine and m1 and posterior to m3. The premolars are more crowded, anteroposteriorly compressed, and rotated slightly posteriorly in the fossils and *E. underwoodi.* In these two forms, the p4 overlaps the posterior edge of p3, which has a distinct notch for the reception of p4, and the anterior cingulum of m1 overlaps the posterior edge of p4. The premolars are less crowded in *E. perotis,* with essentially no overlap between p4 and p3 and only a slight overlap of p4 and m1. The premolars are also more conical and much higher than broad in *E. underwoodi* and the fossils, whereas in *E. perotis* the premolars are shorter and more triangular. The coronoid process rises dorsally almost immediately posterior to the m3 in *E. underwoodi,* whereas in *E. perotis* the horizontal ramus extends farther posterior to the m3 before the coronoid process begins. The ventral edge of the horizontal ramus is distinctly convex ventral to m2 and m3 and then curves sharply dorsally posterior to m3 in the fossils and *E. underwoodi.* The ventral margin of the ramus is nearly straight in *E. perotis,* except where it curves dorsally just posterior to m3. The basal portion of the angular process of the most complete fossil mandible is considerably more massive and located farther anteriorly below the posterior edge of the coronoid process than in *E. perotis,* both of which ally it with *E. underwoodi.*

The two fossil mandibles from the Lecanto 2A fauna are very similar in morphological features and size to mandibles of *Eumops underwoodi.* The measurements of the fossils fall within the range of variation of *E. underwoodi* in all but two dental measurements in which the fossils are slightly larger (table 9). Specimens of *E. underwoodi sonoriensis* from Arizona and northern Mexico are somewhat smaller than individuals of *E. u. underwoodi* from the southern portion of the species range in southern Mexico, Belize, Honduras, and Nicaragua (Eger, 1977). The large size of the Florida fossils suggests that this extinct population was more likely derived from tropical Middle America than from the population that inhabits Arizona and northern Mexico.

DISCUSSION

Peninsular Florida possesses the most complete late Pliocene and Pleistocene fossil

record of land vertebrates in eastern North America. Florida late Blancan sites such as Haile 15A (Robertson, 1976), Santa Fe River 1, and Macasphalt Shell Pit (Morgan and Ridgway, 1987) and early Irvingtonian sites such as Inglis 1A (Webb and Wilkins, 1984) and Leisey Shell Pit 1A (Hulbert and Morgan, 1989; Webb et al., 1989) document some of the earliest arrivals in North America of South American mammals that dispersed northward across the Panamanian Isthmus following the beginning of the Great American Faunal Interchange in the late Pliocene about 2.5 Ma ago (Webb, 1976, 1985; Marshall et al., 1979). Late Pliocene and early Pleistocene Neotropical immigrants recorded from Florida include the armadillos *Dasypus* and *Holmesina*; the glyptodont *Glyptotherium*; the ground sloths *Eremotherium, Glossotherium,* and *Nothrotheriops*; the porcupine *Erethizon*; and the capybara *Neochoerus.* With the exception of the Rancholabrean, the Plio-Pleistocene distribution of these Neotropical mammals elsewhere in the southeastern United States is incompletely known. Blancan and Irvingtonian faunas are rare on the Gulf Coastal Plain between Mexico and northern peninsular Florida and on the Atlantic Coastal Plain north of Florida.

In addition to species directly involved in the Interchange, other mammals now restricted to tropical America occurred in Florida during the Pleistocene. Four living species of nonvolant Neotropical mammals recorded from Florida Pleistocene faunas are no longer found in eastern North America: jaguar, *Panthera onca*; ocelot, *Felis pardalis*; margay, *Felis wiedii*; and hog-nosed skunk, *Conepatus leuconotus.* There are nine species of bats with Neotropical affinities known from Florida. Three of these bats still inhabit the state, whereas the remaining six species occur only in Pliocene and Pleistocene fossil sites. Outside of peninsular Florida there are no other Late Cenozoic records of Neotropical bats in the southeastern United States.

To better understand the geographic origin of Florida's Neotropical bats, it is helpful to define the subdivisions and boundaries of the Neotropics. Hershkovitz (1958) divided the Neotropical Region into the Brazilian, Patagonian, and West Indian subregions. The Patagonian Subregion is composed of the temperate regions of southern South America, the West Indian Subregion is restricted to the Antillean islands, and the Brazilian Subregion comprises virtually the entire continental portion of the New World tropics from Mexico to Brazil. Herskovitz further subdivided the Brazilian Subregion into four provinces. Of these only the Middle American Province is discussed here, as it includes the northern boundary of the Neotropical Region in Mexico.

Koopman and Martin (1959) placed the northeastern boundary of the Neotropical mammal fauna between 23 and 24°N latitude in the southern half of the state of Tamaulipas, Mexico, corresponding to the disappearance of tropical deciduous forest. Thorn forest extends northward along the Gulf Coast into southern Texas, but this northernmost lowland tropical vegetation type is poor in tropical mammals, especially bats (Koopman and Martin, 1959). Koopman (1961) showed that many Neotropical bats occur farther north along the Pacific Coast of western Mexico in the states of Sinaloa and Sonora than they do along the Gulf Coast in Tamaulipas. Koopman (1961: 537) noted: "Sixteen species of bats with an essentially Neotropical distribution, but not reaching the United States, have now been recorded from the five states of western Mexico lying chiefly north of the Tropic of Cancer. Most of these Neotropical bats reach the northern limits of their distribution in southern Sonora and southern Chihuahua at about 28°N."

The subtropical zone of southern peninsular Florida and the closest tropical region on the mainland in Mexico are currently separated by a distance of about 3000 km around the northern rim of the Gulf of Mexico. During the maximum extent of the terminal Pleistocene (Wisconsinan) glaciation about 17 ka ago, sea level was approximately 100 m lower that at present (Bloom, 1983). The Florida peninsula was more than twice its current breadth at that time and included what are now the Florida Keys extending south almost to the Tropic of Cancer (23°27′N). The southwesternmost extension of the Florida peninsula would have been separated from the Yucatan Peninsula of Mexico by as little as 400 km across the Gulf of Mexico during the late Pleistocene, about half the present

distance. It is conceivable, although rather unlikely, that bats dispersed across this narrower water gap. Florida was also situated much closer to several West Indian islands during Pleistocene glacial intervals. Only slightly more than 100 km would have separated the southern tip of the Florida peninsula and the northern coast of Cuba during the late Pleistocene, whereas the distance from the Atlantic Coast of Florida to the Bahamas at that time was as little as 60 km.

The southern half of the Florida peninsula and the Florida Keys are between 28 and 24°N latitude (fig. 1), and thus could theoretically support some species of tropical bats that survive at similar latitudes in Mexico. South Florida and the southern Gulf Coastal Plain of Texas are the only tropical, or perhaps more accurately subtropical, regions in the continental United States. If Florida were directly connected with a tropical region to the south (which, of course, it is not), the species diversity of bats would be expected to increase as the latitude decreased, because the tropics almost always support richer chiropteran faunas than do temperate regions. For example, the bat fauna increases dramatically from the western United States southward into tropical Middle America. Instead, the Florida chiropteran fauna undergoes a marked decrease in species richness in the southern half of the peninsula, indicating that factors other than the subtropical vegetation and climate of South Florida have affected the ability of tropical bats to colonize this region.

One of the primary factors limiting the dispersal of Neotropical bats into southern peninsular Florida and the Florida Keys is the absence of tropical forest vegetation north of Mexico resulting from the temperate climate in the northern Gulf Coastal region between Mexico and southern Florida, most of which is above 28°N. Furthermore, the deep water gaps separating South Florida from the West Indies have severely limited overwater dispersal by Antillean bats. Not only are tropical bats uncommon in South Florida, but several authors have also noted the low diversity of temperate bats in this region (Schwartz, 1952; Jennings, 1958; Layne, 1974; Morgan, 1985). There are several factors that restrict the ability of most temperate bats to colonize South Florida or to survive there. One of the most important of these is the absence of dry caves south of Hernando and Orange counties (approximately 28°30'N) that are suitable for bat roosts (Rice, 1957; Jennings, 1958; Morgan, 1985). The distribution of cave-dwelling bats is consequently limited to the northern half of the Florida peninsula. McNab (1974) proposed that it is difficult for most species of temperate bats to make the transition to a subtropical or tropical environment, even in the absence of competition from tropical species. According to McNab, the most important factor limiting the southern distribution of temperate bats is their inability to adapt to warm winter temperatures, particularly in species that regularly hibernate. The presence of at least six additional species of Neotropical bats in Florida Pliocene and Pleistocene faunas and the wider occurrence of several temperate species strongly indicate that the factors currently limiting bat distributions in the state have not remained constant throughout the past 2 million years.

North American late Pleistocene faunas are often characterized by the coexistence of mammal species that are presently allopatric and presumably ecologically incompatible. These so-called disharmonious faunas existed during times when the climate was more equable than at present, with reduced seasonal temperature extremes. Disharmonious vertebrate faunas were apparently adapted to unique climatic and vegetational conditions that no longer exist in the region where the fossils occur (Graham and Lundelius, 1984). The presence of unique geomorphic features may also have contributed to the formation of disharmonious faunas in the late Pleistocene; an example is the occurrence of extensive cave systems in South Florida where none exist today. The classic disharmonious Pleistocene faunas are found in the Great Plains and Appalachian regions. These faunas contain species of mammals representing temperate habitats occurring with species now characteristic of boreal forest or even tundra habitats far to the north (Graham and Lundelius, 1984).

Although it might seem logical that Florida Pleistocene faunas from glacial intervals

would contain species of north temperate mammals that migrated south with the advancing glaciers, this is not the case. Florida's disharmonious Pleistocene faunas are characterized by the coexistence of south temperate species, primarily mammals still found in the state today, and either tropical forms or species found in the arid regions of western North America. These two types of disharmonious faunas are often difficult to separate because some of the species found in the arid Southwest also occur widely in tropical America. Tropical and western species of mammals and birds are most common in Florida Pleistocene faunas representing glacial intervals, particularly the latest Pleistocene Wisconsinan glaciation. Temperate, tropical, and arid species of vertebrates that are now ecologically incompatible coexisted in the late Pleistocene of Florida, presumably owing to the presence of unique climatic conditions, including milder winters and a drier savanna vegetation (Graham and Lundelius, 1984; Watts and Hansen, 1988).

The Recent and Plio-Pleistocene Chiroptera of Florida were derived from four different geographic regions: (1) eastern North America, (2) western North America, (3) Middle America, and (4) the West Indies. Among the 23 species of Recent and Plio-Pleistocene bats recorded from Florida, 14 species are temperate North American bats that are characteristic of the eastern United States, two species are of West Indian origin, and two bats were derived from Middle America. The geographic origin of the remaining five species of Florida bats is ambiguous because of their widespread distribution or uncertain systematic relationships. One of these bats was derived from either the West Indies or Middle America, three species originated in western North America or Middle America, and one species could have had its origins in western North America, Middle America, or the West Indies.

The temperate bats found in Florida are all widespread species in the southeastern United States that entered the peninsula from the north (table 1). No extirpated species of temperate bats are known from Florida Pleistocene faunas, although several minor range extensions have been documented. *Myotis austroriparius* and *Eptesicus fuscus* are found in two late Pleistocene sites in Dade County several hundred kilometers south of the present southern limit of their ranges in central Florida. *Myotis grisescens* occurs in the late Pleistocene Devils Den fauna in Levy County some 300 km southeast of its current southernmost occurrence in Jackson County along the Alabama line (Martin and Webb, 1974; McNab, 1974). The absence of additional species of north temperate cave bats indicates that the climatic conditions in Florida presently limiting the southern distribution of temperate bats, specifically the mild winters, were probably characteristic of the Pleistocene as well.

Bats with western and Middle American affinities reached Florida from the west by way of the Gulf Coastal corridor (Webb and Wilkins, 1984). The co-occurrence of Middle American tropical species and taxa now restricted to the arid region of the western United States is typical of certain Florida late Pliocene and Pleistocene sites. Among nonvolant mammals, western forms found in Florida Pleistocene faunas include species of the jackrabbit *Lepus,* the pocket gopher *Thomomys,* and the ground squirrel *Spermophilus* (Webb and Wilkins, 1984). This western fauna also includes three species of birds that still inhabit dry scrub or grassland habitats in Florida: the Scrub Jay *Aphelocoma coerulescens,* the Burrowing Owl *Athene cunicularia,* and the Crested Caracara *Polyborus plancus.* The Burrowing Owl and Crested Caracara are also widely distributed in the Neotropical Region, including the West Indies. Bats exhibiting a similar distributional pattern include *Mormoops megalophylla, Eumops underwoodi,* and *Tadarida brasiliensis,* the first two of which are now extinct in Florida. Although the modern ranges of these three bats extend northward into the arid Southwest, and into the Southeast in the case of *T. brasiliensis,* they are principally Neotropical species.

The extinct Florida population of *Eumops underwoodi* entered the peninsula from the west by way of the Gulf Coastal corridor. This species is now restricted to the southwestern United States and Middle America, from Arizona south to Nicaragua. The fossils from the Rancholabrean Lecanto 2A fauna in cen-

tral Florida are near the maximum size for *E. underwoodi,* and as such are most similar to specimens from the tropical portion of the species range from central Mexico to Nicaragua.

Tadarida brasiliensis cynocephala from Florida and the southeastern United States is more closely related to *T. brasiliensis mexicana* from the southwestern United States and Mexico than to any of the smaller West Indian subspecies. *T. brasiliensis* or a closely related form is recorded from Florida shortly after the beginning of the Interchange based on a late Blancan record from the Macasphalt Shell Pit LF in southwestern Florida (Morgan and Ridgway, 1987). Although *Tadarida* almost certainly reached Florida from the west via the Gulf Coastal corridor, it is not possible to determine whether it was derived from the western United States or Middle America.

The two extinct vampire bats recorded from Florida fossil sites—the late Pliocene and early Pleistocene *Desmodus archaeodaptes* and the larger late Pleistocene *D. stocki*—are both related to the living continental Neotropical vampire *D. rotundus* (Morgan et al., 1988; Ray et al., 1988). *D. rotundus* does not presently occur in the West Indies, but is known from two Late Quaternary deposits on Cuba (Koopman, 1958; Wolosyzn and Mayo, 1974). The oldest record of *Desmodus* is from the latest Pliocene Inglis 1A site in central Florida. This fauna is characterized by a large number of South American Neotropical immigrants, indicating that *Desmodus* probably reached Florida via Middle America as an early participant in the Great American Interchange.

The most widespread living species of *Antrozous, A. pallidus,* is now found in desert regions of the American Southwest, whereas *A. dubiaquercus* and *A. koopmani* are Neotropical forms confined to Middle America and the West Indies, respectively. The geographic origin of the large extinct species of *Antrozous* from the latest Pliocene Inglis site is unclear; however, this fauna is characterized by a large influx of both western and Neotropical immigrants.

The recent discovery in the Monkey Jungle Hammock fauna of *Pteronotus* cf. *P. pristinus,* an extinct species of mormoopid bat with indisputable Antillean affinities, suggests the possibility of a West Indian origin for some other Recent and fossil Neotropical bats found in Florida. *P. pristinus* is known elsewhere only from a Late Quaternary cave deposit in Cuba (Silva Taboada, 1974). It is surprising that West Indian bats have not been reported from the Recent and Pleistocene fauna of southern Florida more frequently, considering the close proximity of these two regions. Cuba and the Bahamas are the most likely sources for West Indian bats that may have dispersed to Florida.

The origin of the supposed Florida Keys population of the Neotropical fruit bat *Artibeus jamaicensis* cannot be positively established because there are no Florida specimens known. However, overwater dispersal from Cuba is the most likely possibility, because this large island supports the closest viable population of *A. jamaicensis.* This species is also widespread in the mainland Neotropics from Mexico southward, but it seems unlikely that *A. jamaicensis* could have reached the Florida Keys from the north by dispersing around the Gulf of Mexico. The climate in the northern Gulf Coast region during the Pleistocene would have been too temperate to sustain the year-round supply of tropical fruit necessary for the survival of *A. jamaicensis.*

The origin of the Recent endemic Florida subspecies of *Eumops glaucinus* cannot be clearly established because both the West Indian and mainland Neotropical representatives of this bat have been referred to the nominal subspecies (Eger, 1977). Several authors have suggested that *E. glaucinus floridanus* could have been derived from Cuba, the closest island that supports an extant population of the species (Layne, 1974; Baker and Genoways, 1978; Morgan, 1985). However, it is also possible that *E. glaucinus* reached Florida by the range expansion of the closest mainland population in central Mexico. *E. glaucinus* could have dispersed northward around the northern margin of the Gulf of Mexico to Florida, as did many other species of continental Neotropical mammals found in Florida Pleistocene faunas, including *E. underwoodi.* Unlike *Artibeus jamaicensis,* both species of *Eumops* known from the late Pleistocene of Florida are large in-

sectivorous bats that could have survived in the region along the northern portion of the Gulf Coastal corridor under more equable, but not necessarily tropical, climatic conditions. *E. glaucinus* has inhabited peninsular Florida since at least the Rancholabrean, when it occurred in Brevard County on the Atlantic Coast (Allen, 1932; Morgan, 1985), over 100 km north of its northernmost Recent occurrence.

Although now extinct in Florida, *Mormoops megalophylla* has been identified from three late Pleistocene cave deposits in the central and southern portion of the peninsula. *M. megalophylla* could have dispersed to Florida from the West Indies, although this species also occurs in Middle America and the southwestern United States. *M. megalophylla* is extinct in the West Indies, but it has been recorded from Late Quaternary fossil deposits on Cuba and Andros, both of which are located very close to South Florida (Morgan, 1989). Measurements and comparisons of the Florida fossils of *M. megalophylla* do not conclusively establish the systematic and zoogeographic affinities of this population. Either a West Indian or a continental origin is equally plausible based on available fossil evidence.

Layne (1974) offered several suggestions to explain the rarity of West Indian bats in South Florida, including their inability to cross water barriers and the lack of suitable tropical habitats in the region. However, more than half (61%) of the vascular plants found in the Florida Keys, and the Florida peninsula south of Lake Okeechobee are tropical in origin, 91 percent of which are species that occur in the Caribbean area (Long and Lakela, 1971; Long, 1974). Humphrey and Brown (1986) inferred that the highly seasonal environment of the Florida Keys might limit fruit availability at certain times of the year, thus excluding frugivorous bats. Lazell (1989) pointed out that fruit of the fig *Ficus,* a favored food of *Artibeus jamaicensis,* occurs in the lower Florida Keys throughout the year. There are two native *Ficus* in South Florida, both of West Indian origin. The strangler fig, *F. aurea,* produces fruit throughout the year, whereas the wild banyan tree, *F. citrifolia,* bears fruit only in spring and summer (Long and Lakela, 1971). In addition to factors mentioned by other authors, the current absence of dry caves in South Florida excludes mormoopids, natalids, brachyphylline phyllostomids, and other Antillean cave-dwelling forms.

The late Rancholabrean Monkey Jungle Hammock and Cutler Hammock faunas in Dade County in southernmost peninsular Florida contain four species of bats that no longer occur south of Lake Okeechobee. *Mormoops megalophylla* and *Pteronotus* cf. *P. pristinus* are Neotropical mormoopids now extinct in Florida, whereas *Myotis austroriparius* and *Eptesicus fuscus* are temperate vespertilionids now restricted to the northern two-thirds of the state. The disappearance of these four species of bats confirms that the chiropteran fauna of South Florida has changed considerably in the last 10,000 years. The two mormoopids and *M. austroriparius* are obligate cave dwellers, implying that both the Monkey Jungle and Cutler sites were dry caves or sinkhole/cave systems in the late Pleistocene. Both sites now consist of small, shallow sinkholes.

The geomorphology of southern peninsular Florida and the Florida Keys in the late Pleistocene differed significantly from the current landscape. Sea level was as much as 100 m lower than at present during the Wisconsinan glaciation (Bloom, 1983), and water tables throughout Florida were much lower as well. Watts and Hansen (1988) suggested that water tables in peninsular Florida were between 26 and 31 m lower 15 ka ago, based on evidence from cores taken in deep lakes. Only lakes deeper than about 20 m would have persisted in the late Pleistocene, whereas most shallower lakes and swamps would have been dry. Instead of the vast low-lying wetlands such as the Everglades and Lake Okeechobee that now characterize much of South Florida, this region probably consisted of an extensive grassland savanna as much as 100 m in elevation during the late Pleistocene. Furthermore, southernmost peninsular Florida and the Keys are underlain by late Pleistocene (last interglacial) oolitic and reefal limestones that were highly susceptible to the formation of caves, sinkholes, and other karst geomorphic features during periods of low sea level and low regional water tables.

The abundant remains of cave-dwelling bats in the Rancholabrean Cutler Hammock

and Monkey Jungle Hammock faunas provide independent evidence of large cave systems in South Florida during the late Pleistocene. The rise in sea level and water tables since the end of the Pleistocene caused the flooding of dry caves in South Florida, resulting in the localized extinction of *Mormoops megalophylla, Pteronotus,* cf. *P. pristinus,* and *Myotis austroriparius.* Late Pleistocene and Holocene extinctions of cave-dwelling bats have been documented throughout the West Indies as well, particularly on small low limestone islands such as the Bahamas and Cayman Islands. These localized extinctions in the West Indies have also been attributed to the postglacial flooding of extensive cave systems that were dry during the latest Pleistocene low sea level stand (Morgan and Woods, 1986; Morgan, 1989).

It is instructive to briefly review the zoogeographic affinities of the Florida avifauna, as birds are the only other group of land vertebrates whose dispersal capabilities are similar to those of bats. A Neotropical influence is also apparent in the Recent terrestrial avifauna of peninsular Florida, particularly in South Florida and the Florida Keys (Robertson and Kushlan, 1974). Twelve species of Recent land birds found in Florida were derived from the Neotropical Region, including seven species of West Indian origin, two species found primarily in the mainland Neotropics that probably originated in Middle America, and three species that could have been derived from either the Antilles or Middle America. The seven species with Antillean affinities are the White-crowned Pigeon (*Columba leucocephala*), Mangrove Cuckoo (*Coccyzus minor*), Smooth-billed Ani (*Crotophaga ani*), Antillean Nighthawk (*Cordeiles gundlachii*), Gray Kingbird (*Tyrannus dominicensis*), Black-whiskered Vireo (*Vireo altiloquus*), and Yellow Warbler (*Dendroica petechia*). An additional 21 species of West Indian birds have been recorded from Florida on one or more occasions, but have failed to establish resident breeding populations (Robertson and Kushlan, 1974: table 5). The Short-tailed Hawk (*Buteo brachyurus*) and Black-shouldered Kite (*Elanus caeruleus*) were probably derived from Middle America, although the latter species occurs in the southwestern United States as well. It is difficult to determine the exact origin of the Florida populations of three species of principally Neotropical birds that occur in both the West Indies and in Central and South America: the Snail Kite (*Rostrhamus sociabilis*), Crested Caracara (*Polyborus plancus*), and Burrowing Owl (*Athene cunicularia*). The Crested Caracara and Burrowing Owl are also found in the western United States, but do not occur between peninsular Florida and Texas. The rich Pleistocene record of fossil birds in Florida adds at least eight more species with mainland Neotropical affinities, but no additional West Indian forms (J. Becker, personal commun.).

The Neotropical influence in Florida fossil vertebrate faunas dates back to the beginning of the Great American Faunal Interchange about 2.5 Ma ago, discounting the arrival by overwater dispersal of two genera of South American ground sloths about 9 Ma ago (Webb, 1985). Despite the common occurrence of mainland Neotropical mammals and birds in Florida Pliocene and Pleistocene faunas, there is little compelling evidence that the northern boundary of the Neotropical Region extended much farther north or east during the past 2.5 million years. Rather, the fossil record suggests that a limited number of species of continental Neotropical land vertebrates expanded their ranges northeastward around the northern Gulf Coast and into Florida at various times throughout the late Pliocene and Pleistocene, presumably in response to changing climatic conditions. The only Neotropical mammal that has naturally expanded its range from Middle America into Florida since the end of the Pleistocene is the armadillo *Dasypus novemcinctus.*

Other Neotropical birds and bats immigrated to Florida from the West Indies, as did at least one species of nonvolant vertebrate, the green anone *Anolis carolinensis.* The fossil record does not clearly document when most of these Antillean species arrived in Florida. None of the Antillean birds known from Florida has a fossil record there, whereas *Anolis carolinensis* (Auffenberg, 1956), *Pteronotus* cf. *P. pristinus,* and several other bats with possible Caribbean affinities have been identified from Rancholabrean faunas in the state. The late Pleistocene was perhaps

the most likely time period for colonization by Antillean taxa because the water gaps that now separate South Florida from Cuba and the Bahamas would have been narrower, thereby increasing the likelihood of overwater dispersal. Also, the presence of extensive cave systems in South Florida during the late Pleistocene would have allowed obligate cave-dwelling bats, which comprise a significant portion of the Antillean chiropteran fauna, to inhabit this region. Several species of West Indian birds (Robertson and Kushlan, 1974), and possibly *Artibeus jamaicensis* as well, have colonized Florida from the West Indies only within the past several hundred years. Under the current climatic regime, future immigration of Neotropical vertebrates into Florida will likely be primarily from the West Indies, based on the geographic proximity and similarity in climate and vegetation of these two regions. Dispersal of Neotropical vertebrates into Florida from Middle America is presently limited by the temperate climate and lack of tropical forest vegetation along the northern Gulf Coast.

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Mammals of the Tres Marías Islands

DON E. WILSON[1]

ABSTRACT

The Tres Marías Islands are a chain of four islands trending northwesterly on a line extending from the border of the states of Nayarit and Jalisco, from 80 to 100 km west of the Mexican mainland between 21 and 22°N and 106 and 107°W. The native terrestrial mammal fauna comprises one marsupial, eight bats, one rabbit, one raccoon, and two rodents, one of which probably is now extinct. Three dolphins and one whale are common in the waters surrounding the islands. Several other whales are occasional visitors to these waters, and a sea lion previously recorded no longer occurs there. Endemism is high, with five endemic species, two of which are polytypic on the islands. There are four endemic subspecies, leaving only four broadly distributed bats that are not endemic. The status of *Oryzomys nelsoni* is unresolvable, because it is known only from a few specimens and is now presumed extinct.

Biogeographic affinities of the fauna are southern, with several mainland counterparts limited to the subtropical and tropical coastal areas of western Mexico. Although the bats may have colonized at various times, the terrestrial forms probably became established early, perhaps at a time when lower sea levels reduced the distance from the mainland.

Taxonomic changes include the naming of one new subspecies, *Artibeus intermedius koopmani,* and the recognition of *Rhogeessa parvula parvula* as a subspecies distinct from the mainland form, *R. p. major.*

INTRODUCTION

One of the more interesting segments of the mammal fauna of the Mexican state of Nayarit lives on the Tres Marías Islands, some 100 km off the west coast of Mexico (Bogan, 1978; Diersing and Wilson, 1980; Carleton et al., 1982). Previous surveys of these islands, primarily those of Nelson and Goldman (Nelson, 1899a, 1899b), indicated a highly endemic mammal fauna with many species having unclear relations with their mainland counterparts. I spent most of March 1976 with a Biological Survey field party studying the mammals on the Tres Marías. We verified the occurrence of 13 of the 15 species previously reported from the islands, and gathered evidence that suggests that one endemic species is extinct.

ACKNOWLEDGMENTS

Colleagues who accompanied me to the islands included Dr. Robert L. Brownell, Jr., Dr. Kenneth N. Geluso, Biólogo Pedro Huerta, Dr. C. Brian Robbins, and Dr. Norman J. Scott, Jr. All worked tirelessly in the collection and preparation of mammal specimens, and I am truly grateful to them. We were transported to and between islands on the sailing vessel *Victoria,* crewed by Richard Blake and Mary Keller.

Many others contributed to our work on the Tres Marías Islands. Necessary collecting permits and a variety of administrative assistance were provided by Mário Luis Cossio Gabucio, Director General, and J. Ticul Alvarez Solorzano, Asistente Tecnico, both then with the Dirección General de la Fauna Silvestre of Mexico. El Lic. Sérgio García Ramírez, then Subsecretario de Gobernación, arranged for us to work in the islands. We were admirably assisted by many employees and inhabitants of the penal colony on María Madre. I am grateful to Lic. Carlos Pellico Daroca, Director Interino, Ing. Guillermo

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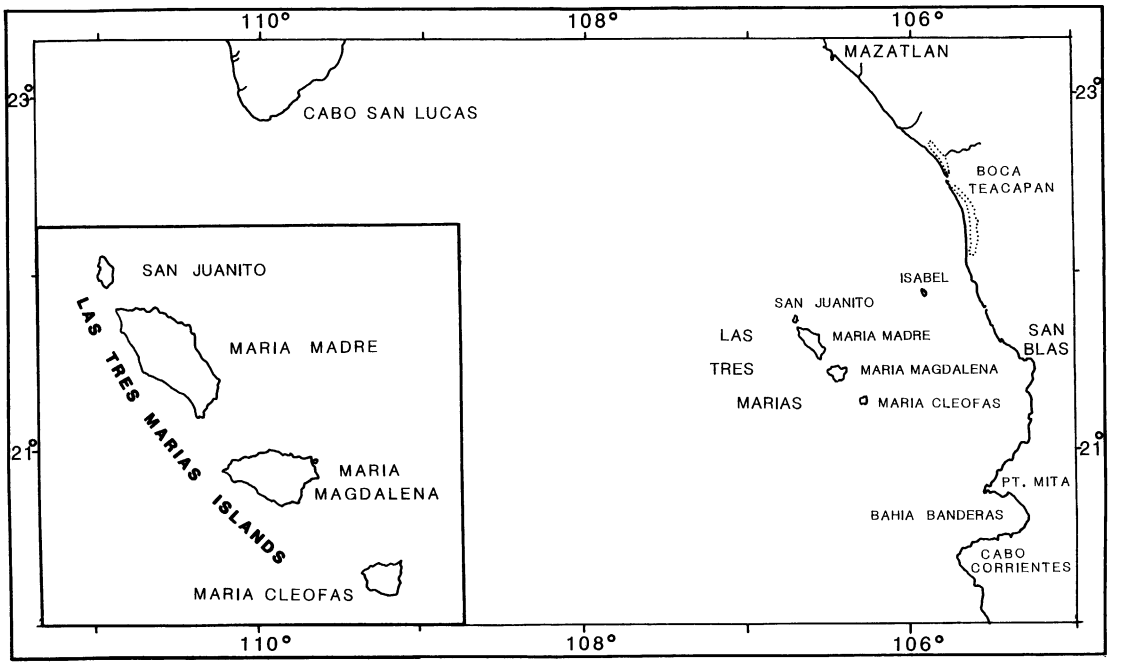

Fig. 1. The Tres Marías Islands and adjacent mainland.

Cuevas Sánchez, Cristóbal Castillo Nuñez, and Francisco Garzón Gomez for logistical assistance. The following involuntary residents of María Madre gave us field assistance and shared their knowledge of the natural history of the islands: Guadalupe Flores Castro, Bartolo Sánchez Soriano, Rolando de Hoyos Martínez, Juan Beltruy Cetina, and Gilberto Duarte Rivas.

Robert J. Baker kindly provided the raw data for the samples of *Macrotus waterhousii bulleri* used in Davis and Baker (1974).

STUDY AREA

The Tres Marías Islands, lying west of the Mexican mainland and southeast of the Baja California peninsula between 21 and 22°N and 106 and 107°W (fig. 1), are the largest islands off the west coast of Central America south of the Sea of Cortez. The Tres Marías are a chain of four islands trending northwesterly on a line extending from the border between Nayarit and Jalisco. The closest mainland point is Punta Mita on the northern edge of Banderas Bay in Nayarit. María Cleofas is 80 km from Punta Mita, María Magdalena 105 km, María Madre 130 km, and San Juanito 150 km. San Juanito is the farthest offshore, about 112 km due west of the mainland. The geography, geology, and paleontology of the islands are poorly known. Even the position of the islands on some sailing charts is inexact.

The sea bottom slopes gradually out from the mainland to a depth of more than 200 fathoms, then rises abruptly at the islands. On the seaward side, the bottom falls off abruptly to more than 2300 fathoms. A submerged peak at 35 fathoms lies on the line of the islands between Punta Mita and María Cleofas.

San Juanito is the smallest and northwesternmost island, separated from María Madre by a shallow channel about 3 km wide (fig. 2). It is approximately 5 km long and 2 km wide, with a maximum elevation of about 50 m. The elevated portion of the island away from the beach is covered with dense stands of trees, bushes, and agaves about 3–4 m in height (fig. 3). Sisal is grown here and occasionally harvested by people from María Madre, but the island is otherwise uninhabited (fig. 4). There appears to be no fresh water

Fig. 2. María Madre Island as seen from San Juanito. The 3-km-wide channel seen here apparently serves as an effective barrier to *Sylvilagus graysoni,* which is represented by separate subspecies on these two islands. Note the numerous introduced sisal plants in the foreground.

on the island, although an old cistern near the beach held rain water.

María Madre, the largest island of the chain, is 23 km long and 5–10 km wide. The maximum elevation is slightly more than 600 m. Pleistocene limestones and sandstones, 135 m thick, are underlain by 300 m of Miocene diatomaceous shales. These shales are in turn underlain by diorite and finally by granite. The southern end of the island appears to be an uplifted Pleistocene beach. Hanna (1926: 69) described the central portion of the island as follows:

> The center of the mountain mass which forms María Madre Island was found to consist of granite chiefly, with a rim of diorite around the edges. This whole mass was land during part of the Pliocene because many boulders of granite are in the sediments of that age. The main cañons have cut into this granite about 300 feet or more. Near the top of the island the Pliocene sediments are only about 50 feet thick, but they increase to about 300 feet toward the shore. The prevailing dips seem to be away from the center of the island. During a portion of Pliocene time large coral reefs existed around this old land mass and large blocks of the fossiliferous material, firmly cemented, have fallen down from the exposure and have rolled indiscriminately far out into the forest.

Nevertheless, the reefs are found only on the northern and eastern sides, suggesting that the landmass was peninsular or even insular.

In coastal areas, the natural vegetation is tropical deciduous forest with a canopy height of 4 m, but human activities have eliminated most of this forest (fig. 5). The interior was originally forested with trees up to 30 m (fig. 6), but lumbering has eliminated much of the harvestable timber (fig. 7). Nelson (1899a: 12) noted: "In its primeval condition, before the advent of woodcutters, it must have presented a fine example of tropical forest growth. Now, only a few specimens remain to show what the original condition must have been."

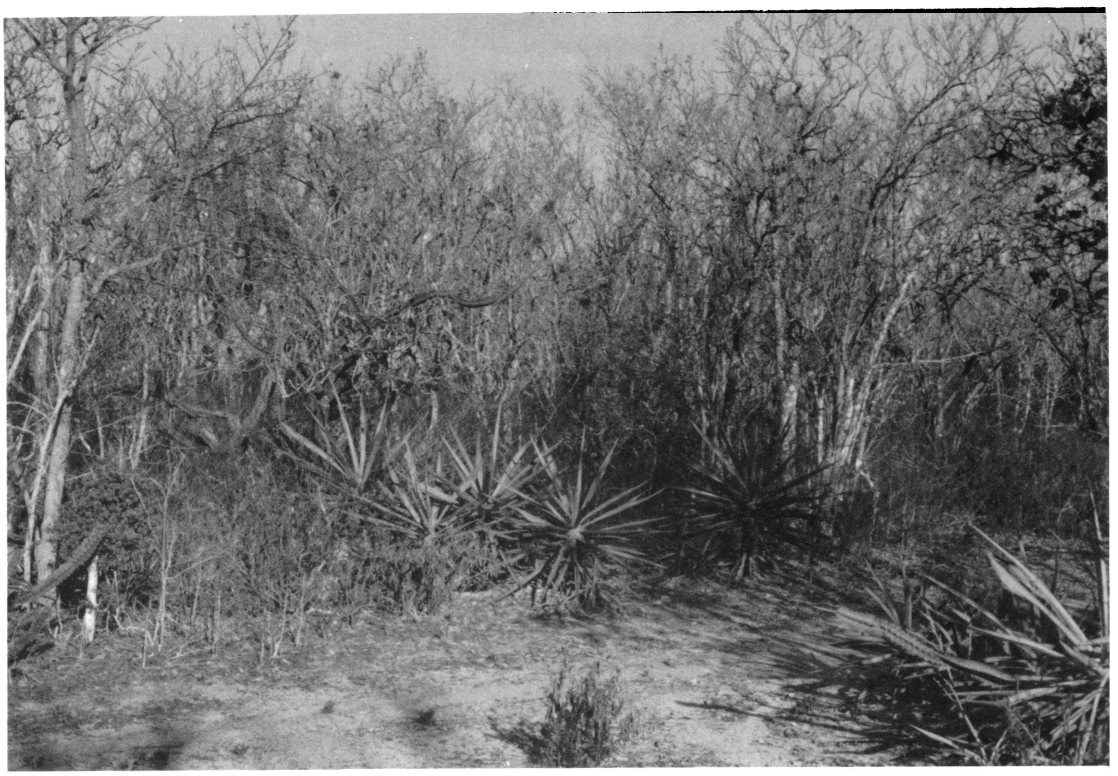

Fig. 3. Dense vegetation on the elevated inland portion of San Juanito. The thorn scrub has overgrown the introduced sisal plants to form an impenetrable thicket. *Sylvilagus graysoni badistes, Marmosa canescens,* and *Peromyscus madrensis* thrive in this habitat.

There are several intermittent streams on the island, and occasional springs in the mountains of the interior. The government of Mexico maintains a penal colony on María Madre, and the total population of the island runs between two and three thousand.

María Magdalena is the second largest island and is separated from María Madre by a channel 8 km wide. The island is 15 km long by 8 km wide, with a maximum elevation of about 500 m. Hanna (1927) found no evidence of the great deposits of Pliocene and Miocene organic shales and limestones that are common on María Madre, and suggested that the two islands have different geologic histories. The forest is less disturbed than on María Madre, as there are no permanent residents. Nelson (1899a: 12) noted: "On María Magdalena the conditions were similar to those on María Madre, but a larger percentage of the original forest still remains intact, although the Spanish cedars are mainly gone." Nearly 60 years later, Stager (1957: 415) reported: "In the past there has been a relatively small amount of timbering on María Magdalena, but the original plant cover has not been altered to any noticeable degree." White-tailed deer (*Odocoileus virginianus*) and domestic goats were introduced on María Magdalena about 1903 (Hanna, 1926). At the time of Stager's visit in 1955, he reported (Stager, 1957: 415): "Magdalena is well covered with vegetation, and as of the above date, the goats do not seem to have caused any appreciable damage by their browsing." However, Zweifel (1960: 87), on a visit in 1957, noted that "Away from the vicinity of the beach there is almost nothing in the way of herbs, and shrubs are infrequent and picked clean by the deer and goats." We found the effects of browsing quite noticeable (fig. 8), much as Zweifel described.

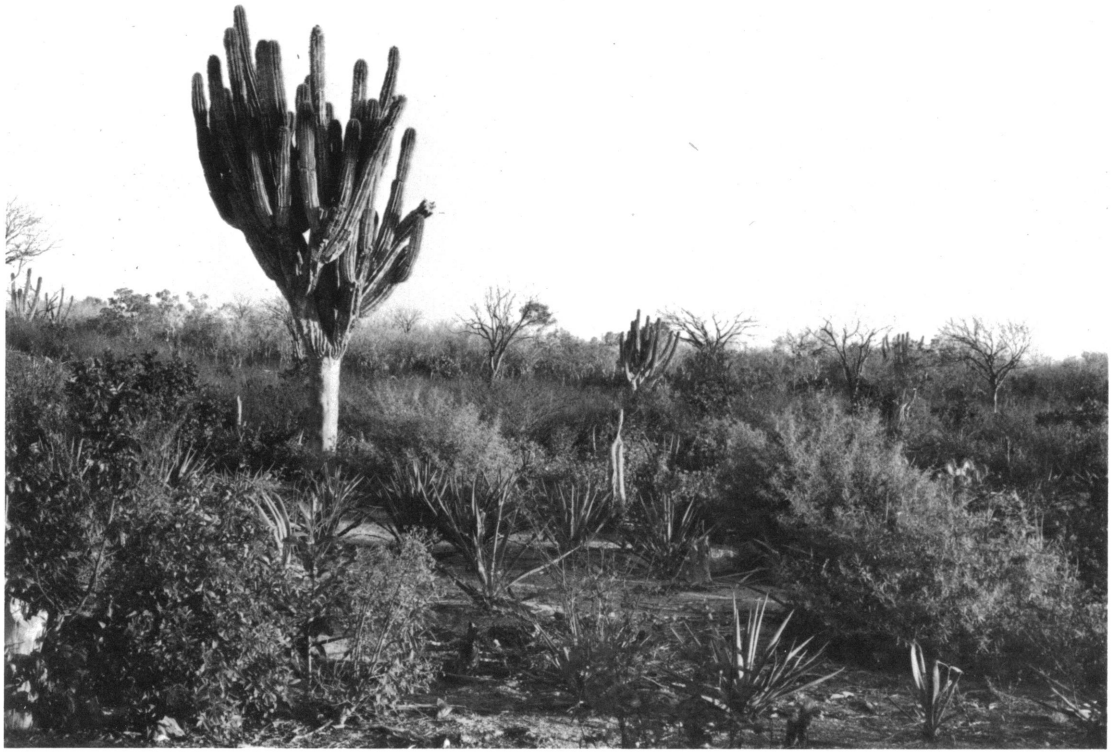

Fig. 4. Remains of a sisal plantation becoming overrun by native vegetation on San Juanito. This area has obviously been cleared more recently than that shown in figure 3. Large columnar cacti were probably left when the sisal was planted.

María Cleofas, the southernmost island, is separated from María Magdalena by a channel of 16 km. The island is essentially round, with a diameter of 5 km and a maximum elevation of 400 m. Nelson (1899a) described the island as rocky and sterile, but Stager (1957: 415) provided a more detailed description: "María Cleofas has a vegetative cover which is almost intact . . . our investigations revealed dense forests on the slopes and level land on the eastern side of the island." María Cleofas is the least disturbed of all the islands and the forest appears to be relatively intact (fig. 9). The only human inhabitants consist of a small detachment of marines who stay near their camp on the eastern side of the island. There are freshwater streams on the island.

The islands are more arid than the mainland. Average yearly rainfall is 635 mm, most of which falls in the summer, often accompanied by violent storms that sweep up from the southeast. On the mainland, Cabo Corrientes receives 952 mm of rain annually and Puerto Vallarta 1484 mm. San Blas, due east of María Madre, receives 1462 mm annually. The mainland area most similar to María Madre is Culiacan, Sinaloa, which receives 605 mm. Culiacan lies in coastal plain thorn forest approximately 400 km north of the Tres Marías.

Temperatures are moderate, with monthly averages ranging from 20.3°C in January and February to 28.1°C in July and August. Recorded extremes are 4.6°C and 37.5°C. These figures are similar to those for San Blas on the mainland.

Pleistocene marine deposits on the three large islands suggest that during at least part of the Pleistocene, the area above water was reduced. San Juanito may have been submerged, but nothing is known of its geologic

Fig. 5. Clearings and second growth on María Madre. Much of the lower reaches of the island is a mosaic of such clearings, interspersed with regrowth from areas probably logged as much as 100 years ago. These areas support only a few individuals of most species of native land mammals.

history. Zoogeographers would particularly like to know whether the islands were ever connected to the mainland. Their geographic position, almost in a line connecting the peninsula of Baja California with Cabo Corrienes to the south of Banderas Bay on the mainland, is suggestive of a possible connection with one or the other. Geologists agree that glacial maxima locked up sufficient water to cause worldwide lowering of the sea level. At the time of most extensive glaciation, sea levels may have been lowered as much as 125 m. Under present conditions, lowering the sea level 125 m would result in the islands being separated from the mainland by 30 km (as opposed to the current 80 km), with a maximum depth of 250 m in the intervening channel. The islands may have been united into a large island about 80 km long, and adjacent to a new island formed between María Cleofas and Punta Mita. Although such a lowering of sea level would not establish a land connection with the mainland, it would facilitate rafting. Local crustal movements in this tectonically active region could have resulted in substantial deviations from these estimates. The differential crustal movement of 300 m needed to establish a land connection is not out of line with others thought to have occurred in Pleistocene times in other parts of North America. In short, what little geologic evidence is available suggests the presence of dry land in the Tres Marías region since the mid-Pliocene. It is unknown if this landmass was always insular or if it was ever connected to the mainland.

HISTORY OF MAMMAL STUDIES ON THE TRES MARÍAS

The Tres Marías Islands were known to early Spanish explorers, and credit for their

Fig. 6. Native vegetation along the upper reaches of Arroyo Hondo on María Madre. The large fig trees were left along a few riparian areas, probably due to their lack of value as timber. The remaining isolated springs and intermittent streams provide refuges for terrestrial mammals and sources of water and food for bats.

discovery goes to Diego de Mendoza, who named them Las Islas de Magdalena in 1532. The islands were also well known to early buccaneers, according to one of them, William Dampier (1729), who mentioned the presence of raccoons (*Procyon insularis*), "*Indian* conies" (most likely *Sylvilagus graysoni*), and seals (probably *Zalophus californianus*) when he visited María Magdalena in 1686. Although mentioned by English exploring expeditions in the 18th and early 19th centuries, the islands remained uninhabited until sometime near the middle of the 19th century, when bandits took refuge there and used the islands as a base from which to raid villages on the mainland (Nelson, 1899a). The first permanent settlement was established by timber cutters attracted by the extensive stands of Spanish cedar (*Cedrela mexicana*), which were first mentioned by Dampier (1729). That settlement was on María Madre, which was leased for timber harvest to Don Andres Somilara by the original Spanish grantee (Grayson, 1871).

The first naturalist to visit the islands was Colonel Andrew Jackson Grayson, who studied birds during three trips in 1865, 1866, and 1867. Grayson (1871) mentioned seeing raccoons, and collected specimens of rabbits later named *Sylvilagus graysoni* by J. A. Allen (1877) and bats later described by H. Allen (1866) as *Rhogeessa parvula.* Alfred Russell Wallace (1876) added the mouse-opossum (*Marmosa canescens*) to the list of mammals known from the islands based on Grayson's observations, and argued that the presence of mammals and reptiles indicated a recent connection to the mainland.

Alphonse Forrer collected specimens for the British Museum on María Madre in 1881. He obtained *Marmosa canescens, Rhogeessa parvula, Lasiurus blossevillii, Myotis findleyi,*

Fig. 7. Dense thorn scrub second growth remaining after timber harvest on María Madre. These areas support populations of native mammals, in spite of their obvious differences from the original tall forest.

Macrotus waterhousii, Glossophaga soricina, Procyon lotor, and *Sylvilagus graysoni* (Thomas, 1881). Thomas also implied that Norway rats (*Rattus norvegicus*) were common on María Madre at that time, but subsequent specimens have all proven to be *Rattus rattus.*

In May of 1897, E. W. Nelson and E. A. Goldman of the U.S. Biological Survey collected 147 specimens of mammals representing 9 species, bringing the total number of species known from the islands to 11. Merriam (1898) described four new taxa based on those collections, which were summarized by Nelson (1899a, 1899b).

An expedition from the California Academy of Sciences visited the Tres Marías Islands in May 1925. Their collections included four species of mammals from the islands (McLellan, 1926). W. H. Burt collected briefly on María Magdalena in February 1938 and deposited specimens in the Museum of Zoology at the University of Michigan, Ann Arbor.

As a member of the Puritan–American Museum of Natural History expedition, R. G. Van Gelder collected 73 specimens from the Tres Marías in March and April of 1957, including a new genus of bats, *Bauerus.* Although several ornithological expeditions have visited the islands, including one from the Los Angeles County Museum in 1955 (Stager, 1957) and several between 1957 and 1963 from the University of British Columbia (Grant and Cowan, 1964), additional work on mammals was not undertaken until our 1976 expedition.

ACCOUNTS OF SPECIES

The synonymies given below include the original description, the first record from the islands, other names that have been applied to the Tres Marías populations, and the first

Fig. 8. Forests on María Magdalena showing obvious lack of undergrowth due to browsing by deer and goats. Although the trees are taller here than on most areas of María Madre, the introduced ungulates have wreaked havoc on the understory vegetation.

use of the current name combination. The synonymies do not include names applied only to mainland populations. Specimens from the Tres Marías Islands are listed under Specimens Examined by island and museum acronym as follows: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Field Museum of Natural History (FMNH), National Museum of Natural History (USNM), Universidad Nacional Autónoma de México (UNAM), University of British Columbia (UBC), and University of Michigan, Museum of Zoology (UMMZ). A summary of the distribution of each species on each island is provided in table 1.

Marmosa canescens insularis Merriam

Didelphys murina: Thomas, 1881: 212. Not *Didelphis murina* Linnaeus, 1758. First record from Tres Marías Islands.

Marmosa insularis Merriam, 1898: 14. Type locality "María Madre Island Mexico."

[*Didelphis* (*Caluromys*)] *insularis:* Matschie, 1916: 37. Name combination.

Marmosa canescens insularis: Tate, 1933: 144. First use of current name combination.

Alphonse Forrer collected the first mouse-opossum on the Tres Marías and sent the specimen to the British Museum (Thomas, 1881). Nelson (1899b) reported these opossums to be common on María Madre, but only at higher elevations. He found them around wild fig trees, where they were feeding on the fruits. We did not find them on María Madre despite considerable trapping effort and looking for nests. We found their nests on María Cleofas and on San Juanito, much as Nelson reported from María Magdalena. Although to date no specimens have been taken from María Magdalena, people living there at the time of Nelson's visit in 1897

Fig. 9. Trail through remaining native forest on María Cleofas. This forest probably best represents the habitat that originally covered the majority of the three largest islands. These are the areas that have been least disturbed by humans or introduced flora and fauna.

described the nests and their inhabitants accurately. These nests are round masses of dry leaves and stems, lined with softer vegetation, and are found in the forks of small trees and bushes 1–2 m above the ground.

One major difference on María Madre between the time of Nelson's visit in 1897 and ours in 1976 is the tremendous increase in density of *Rattus rattus*. We found them in almost all habitats, and I suspect that their presence has led to a decline or extirpation of the mouse-opossums. *Marmosa canescens* are usually easy to detect, and we captured them by hand as they were foraging at night in the shrubby undergrowth on María Cleofas.

This attractive little opossum is similar in size and appearance to its mainland conspecifics, but has a longer tail, a longer but narrower skull, and a more richly fulvous or cinnamon pelage (Merriam, 1898). The fur is long and has a fluffy, silky texture. Dorsally the animal is drab brown with pale fulvous highlights that become conspicuous on the sides of the neck. There are black rings around each eye that extend forward along the sides of the rostrum and border the narrow, medial, buffy-fulvous facial stripe. The venter is buffy cream or yellow, becoming darker on the throat and chest. The feet and tail are pale buffy brown.

Head and body length averages 69% of tail length in 8 *insularis* and 89% in 13 mainland specimens (table 2). In fact, the only overlap is provided by a single specimen collected by Nelson and Goldman at Tepic. Unfortunately, the tail is broken on this specimen, so there is no way to verify the recorded measurement. The skull is similar to that of mainland populations, but longer and more slender (ta-

ble 2). The braincase is more rounded, but the rostrum, palate, and basicranial region are narrower. Significant differences exist in the length of the upper molar row and the width of the nasal bones (Student's *t*-test; table 2).

Marmosa canescens is sexually dimorphic, with males averaging larger than females in most measurements. If males are considered separately, tail length and palatal length also show significant differences between the island and mainland populations (table 3).

Marmosa canescens has a 2n = 22 and FN = 20 karyotype consisting of three pairs of large and seven pairs of medium-sized to small acrocentric autosomes. The X-chromosome is a small acrocentric and the Y is apparently a tiny submetacentric. To date, karyotypes of specimens analyzed show no variation between the islands and the mainland (Engstrom and Gardner, 1988).

Although Merriam believed that these mouse-opossums differed sufficiently from the mainland populations earlier named by J. A. Allen (1893) to warrant specific recognition, Tate arranged them as one of four subspecies. I agree that the insular populations should be considered a subspecies of *M. canescens,* but they are considerably more distinct from the three mainland subspecies than those forms are from each other. Tate (1933: 140) recognized this when he adopted the incongruous arrangement and pointed out: "But since the *canescens, mexicana,* and *mitis* sections must be supposed to have had a common ancestor, which was in all probability a cinnamon-colored form, *insularis* may have become separated before the gray coloration of the other subspecies became established. This is substantiated by the fact that *insularis* is structurally further removed from other subspecies than they are from each other."

Given the degree of differentiation between the island and mainland forms, two logical systematic arrangements are available. The first would be to recognize *insularis* as a distinct species, and leave *canescens* with three subspecies, all about equally differentiated. The second, and one I currently favor, would be to recognize only two subspecies of *canescens,* the nominate form on the mainland and *insularis* on the islands. However, until studies on mainland material are completed, the mainland specimens used for comparisons herein would be referable to *Marmosa canescens sinaloae* J. A. Allen.

TABLE 1

Distribution of the Mammals of the Tres Marías on Each of the Individual Islands[a]

	María Madre	María Magdalena	María Cleofas	San Juanito
Marmosa canescens	NG	?	X	X
Macrotus waterhousii	X	X		
Artibeus intermedius	X	X	X	X
Glossophaga soricina	X	X	X	X
Natalus stramineus		P		
Lasiurus blossevillii	X	X	X	
Rhogeessa parvula	X	X	X	X
Myotis findleyi	X	X	X	
Antrozous dubiaquercus	X	X	X	
Sylvilagus graysoni	X	X	X	X
Rattus rattus	X	X		
Peromyscus madrensis	X	NG	X	X
Oryzomys nelsoni	NG			
Procyon lotor	S	NG		
Odocoileus virginianus		X		

[a] NG, specimens available from Nelson and Goldman expedition; none in 1976. ?, implied in Nelson (1899), but no specimens available. X, specimens available from 1976 expedition. P, specimens available from Puritan expedition in 1957; none in 1976. S, specimen available from Nelson and Goldman expedition; sight record in 1976.

SPECIMENS EXAMINED: María Cleofas Island, 4 (USNM); María Madre Island, 5 (USNM); San Juanito Island, 1 (USNM).

Macrotus waterhousii bulleri H. Allen

Macrotus waterhousii: Thomas, 1881: 207. First record from Tres Marías Islands.

Macrotus bulleri H. Allen, 1890: 93. Type locality "Bolanos, Jalisco, Mexico."

Otopterus mexicanus: Merriam, 1898: 18. Name combination.

Otopterus bulleri: Elliot, 1905: 510. Name combination.

Macrotus mexicanus bulleri: Rehn, 1904: 439. Name combination.

Macrotus waterhousii bulleri: Anderson and Nelson, 1965: 28. First use of current name combination.

TABLE 2
Measurements (in millimeters) of *Marmosa canescens insularis* and *M. c. sinaloae*

	M. c. insularis				*M. c. sinaloae*		
	Mean ± SD	Range	N		Mean ± SD	Range	N
Total length	256 ± 30.0	210–302	8		238 ± 31.0	195–275	13
Tail length	152 ± 17.0	131–182	8		127 ± 17.0	104–152	13
Hind foot length	18 ± 2.0	15–21	8		18 ± 2.0	15–20	13
Ear length	23 ± 2.0	21–26	7		22 ± 2.0	16–25	10
Greatest skull length	31.7 ± 1.5	29.1–33.1	9		30.6 ± 2.4	27.2–34.8	10
Basal length	28.2 ± 1.2	26.3–29.8	9		27.3 ± 2.2	24.3–31.2	11
Zygomatic breadth	16.6 ± 0.9	15.5–17.9	9		16.8 ± 1.5	15.2–20.0	11
Palatal length	17.3 ± 0.8	16.1–18.4	9		16.5 ± 1.1	14.8–18.1	13
Breadth of bulla	2.7 ± 0.2	2.4–3.0	9		2.8 ± 0.1	2.6–3.0	11
Breadth across bullae	9.6 ± 0.6	8.6–10.7	9		9.8 ± 0.5	9.3–10.5	11
Breadth across upper molars	9.8 ± 0.4	9.3–10.7	9		9.8 ± 0.5	9.3–10.7	13
Length of M1–M3	5.5 ± 0.1	5.4–5.7	9	**	5.3 ± 0.2	5.0–5.7	13
Length of nasals	14.7 ± 0.9	13.1–15.9	8		14.0 ± 1.3	12.1–16.5	12
Width of single nasal	2.0 ± 0.1	1.9–2.2	9	***	1.8 ± 0.2	1.6–2.1	13
Postorbital constriction	6.0 ± 0.3	5.7–6.5	9		6.1 ± 0.4	5.0–6.5	12
Breadth of braincase	11.8 ± 0.4	11.2–12.3	9		11.8 ± 0.4	11.2–12.4	10
Mandible length	23.0 ± 1.5	20.8–24.8	9		22.5 ± 1.9	19.8–25.6	12
Length of m1–m4	7.1 ± 0.2	6.7–7.4	9		6.8 ± 0.2	6.5–7.3	12

** Difference between subspecies significant at 0.01 level.
*** Difference between subspecies significant at 0.001 level.

The island fauna contains a single member of each of the three major subfamilies of the family Phyllostomidae. *Macrotus waterhousii* represents the subfamily Phyllostominae. These large-eared bats (fig. 10) feed on fruit and on large insects gleaned from foliage and other substrates. They are common on the two larger islands, María Madre and María Magdalena. Two specimens sent to the British Museum by Forrer (Thomas, 1881) were the first recorded from the islands. Nelson and Goldman found a roost of about 100 individuals in a warehouse on María Madre and collected a large series (Merriam, 1898; Nelson, 1899b). The California Academy of Sciences Expedition collected 12 specimens (McClellan, 1926) from a large roost in a deserted ranch house on the north end of María Madre. The Puritan expedition collected one specimen on María Magdalena in 1957.

We collected *Macrotus* in mist nets set over water holes in Arroyo Hondo on the north end of María Madre and in Arroyo Platanales on the west side. We caught them in similar

TABLE 3
Measurements (in millimeters) of male *Marmosa canescens insularis* and *M. c. sinaloae* Showing Significant Differences

	M. c. insularis				*M. c. sinaloae*		
	Mean ± SD	Range	N		Mean ± SD	Range	N
Tail length	161 ± 15	147–182	5	**	131 ± 15	112–152	8
Width of single nasal	2.1 ± 0.1	2.0–2.1	6	**	1.8 ± 0.2	1.6–2.1	8
Length of M1–M3	5.6 ± 0.1	5.4–5.7	6	*	5.3 ± 0.2	5.2–5.7	8
Palatal length	17.8 ± 0.4	17.4–18.4	6	*	16.9 ± 0.7	15.7–18.1	8

* Difference between subspecies significant at 0.02 level.
** Difference between subspecies significant at 0.01 level.

Fig. 10. *Macrotus waterhousii bulleri* from the Tres Marías.

habitat on María Magdalena as well. On María Magdalena we found a colony of more than a hundred roosting in the cavity formed by the overturned trunk and roots of a large tree bordering a small stream. In spite of considerable effort expended netting similar sites on María Cleofas, we did not encounter *Macrotus* on that island. I suspect that they will eventually be found there. We also failed to collect this species on San Juanito, where the habitat probably is not suitable.

None of the animals we collected in March showed any signs of reproductive activity. However, Nelson (1899b: 18) noted that the specimens he collected in May ". . . were mostly females heavy with young." Only about one-third of our sample consisted of females.

These distinctive-looking bats have a noseleaf, large ears that are united across the head by an interauricular band, and a large tragus (fig. 10). The uropatagium is wide and encloses all but the extreme tip of the tail. The dental formula is I 2/2, C 1/1, P 2/3, M 3/3. The first and second upper molars lack a hypocone, and the first and second lower molars have only a poorly developed hypoconid. The paraconid of the first lower molar is also reduced. The rostrum is not markedly elongated, and is lower than the braincase. In general, specimens from the Tres Marías Islands are smaller than their mainland counterparts. The skulls are short and broad, but more slender in the rostral and palatal areas.

The karyotype of *M. waterhousii* consists of 46 chromosomes and an FN of 60 (Nelson-Rees et al., 1968). Autosomes consist of eight pairs of biarmed and 28 medium-sized to small uniarmed chromosomes. The X is a medium-sized metacentric and the Y is a small acrocentric.

Geographic variation in *Macrotus waterhousii* has been well studied (Rehn, 1904; Anderson and Nelson, 1965; Davis and Baker, 1974; Greenbaum and Baker, 1976; Ray and Wilson, 1979). I used 13 external and cranial measurements to compare the Tres Marías material to mainland specimens of *Macrotus waterhousii bulleri* from the five closest states. Univariate comparisons re-

TABLE 4
Measurements (in millimeters) of *Macrotus waterhousii bulleri*
(Mean ± SD)

Variable	Sonora (N = 50)	Durango/Sinaloa (N = 15)	Nayarit (N = 10)	Jalisco (N = 24)	Tres Marías (N = 42)
Greatest skull length	22.71 ± 0.24	23.74 ± 0.29	23.20 ± 0.27	23.12 ± 0.29	22.87 ± 0.29
Condylobasal length	19.89 ± 0.23	20.61 ± 0.25	20.49 ± 0.21	20.26 ± 0.24	20.17 ± 0.20
Occipitonasal length	19.61 ± 0.24	20.57 ± 0.38	20.19 ± 0.25	20.05 ± 0.28	20.00 ± 0.23
Mastoid breadth	10.09 ± 0.18	10.57 ± 0.21	10.44 ± 0.21	10.32 ± 0.20	10.46 ± 0.10
Braincase breadth	8.45 ± 0.16	8.74 ± 0.21	8.79 ± 0.19	8.60 ± 0.14	8.86 ± 0.12
Interorbital breadth	4.00 ± 0.08	4.01 ± 0.11	4.06 ± 0.14	3.99 ± 0.08	4.07 ± 0.09
Postzygomatic breadth	8.84 ± 0.15	9.12 ± 0.16	9.06 ± 0.14	8.92 ± 0.17	9.11 ± 0.12
Postpalatal length	7.47 ± 0.16	7.74 ± 0.24	7.75 ± 0.14	7.59 ± 0.23	7.67 ± 0.15
Maxillary toothrow length	8.50 ± 0.13	8.90 ± 0.10	8.77 ± 0.10	8.65 ± 0.20	8.59 ± 0.11
Width across upper molars	7.31 ± 0.11	7.66 ± 0.15	7.44 ± 0.15	7.41 ± 0.16	7.31 ± 0.10
Canine breadth	3.52 ± 0.13	3.67 ± 0.15	3.72 ± 0.12	3.57 ± 0.09	3.63 ± 0.10
Forearm length	47.35 ± 4.24	50.13 ± 0.87	49.02 ± 0.90	49.04 ± 1.41	48.73 ± 0.78
Metacarpal 3 length	37.61 ± 0.86	38.58 ± 0.71	38.14 ± 0.76	39.27 ± 3.17	37.65 ± 0.63

vealed the means of most groups, including the Tres Marías group, to differ significantly in most characters (tables 4, 5).

Although differences between mainland and island populations are of sufficient magnitude to warrant nomenclatural recognition, they are of the same magnitude as those between samples from within mainland populations (table 6). Specimens from the islands are most like those from Nayarit, the closest state on the mainland (fig. 11; table 6). On the mainland, the general north–south cline of increasing size identified by Anderson and Nelson (1965) is actually more complicated (see Davis and Baker, 1974). The smallest animals are from the northernmost localities in Sonora, and the greatest step in the cline is between them and their immediate neighbors to the south in Sinaloa and Durango. The largest animals are from Sinaloa and Duran-

TABLE 5
Significances of Differences between Means for 13 Characters Comparing Tres Marías Islands Samples with Several Mainland Samples of *Macrotus waterhousii bulleri*

Variable	Sonora	Durango/ Sinaloa	Nayarit	Jalisco	Mainland total
Greatest skull length	**	***	**	***	***
Condylobasal length	***	***	***		***
Occipitonasal length	***	***	***		*
Mastoid breadth	***	**		***	**
Braincase breadth	***	**		***	***
Interorbital breadth	***	**		***	**
Postzygomatic breadth	***			***	***
Postpalatal length	***				
Maxillary toothrow length	***	***	***		***
Width across upper molars		***	**	**	***
Canine breadth	***		*	*	
Forearm length	*	***			
Metacarpal 3 length		***	*	**	

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

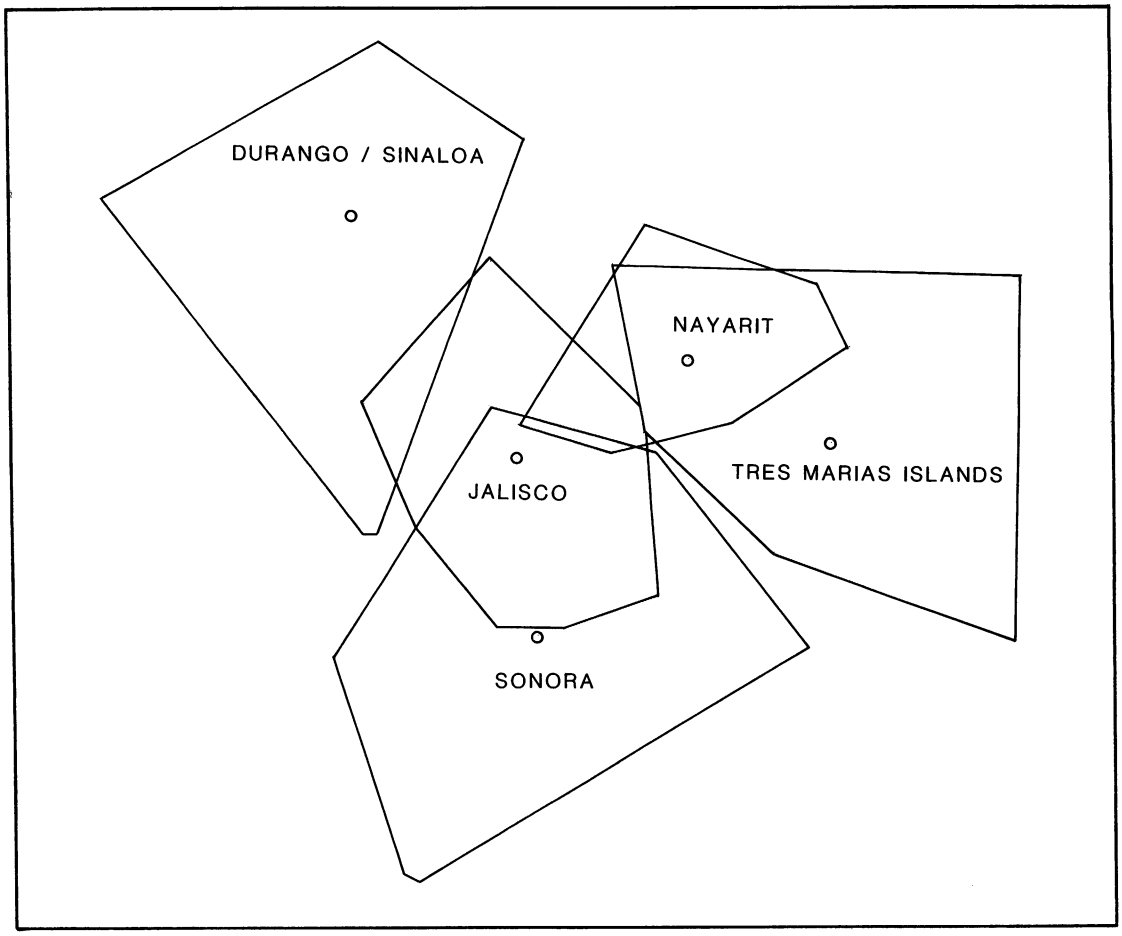

Fig. 11. Plot of canonical variable 1 against canonical variable 2 from a discriminant function analysis of *Macrotus waterhousii bulleri* from the Tres Marías and the adjacent mainland.

go, and size decreases southward to Jalisco. That the smallest animals occur in sympatry with the smaller northern species, *Macrotis californicus,* suggests similar environmental constraints on size in Sonora and northward. Additional study of the amount and kind of variation in this species is warranted.

SPECIMENS EXAMINED: María Madre Island, 59 (USNM), 1 (AMNH); María Magdalena Island, 84 (USNM).

Glossophaga soricina mutica Merriam

Choeronycteris mexicana: Thomas, 1881: 207. Not *Choeronycteris mexicana* Tschudi, 1844. First record from Tres Marías Islands.

Glossophaga mutica Merriam, 1898: 18. Type locality "Maria Madre Id., Tres Marias Ids., Mexico."

Glossophaga soricina mutica: Miller, 1913: 420. First use of current name combination.

TABLE 6

Numbers of Significant Differences in 13 Characters for Various Samples of *Macrotus waterhousii bulleri*

	Tres Marías Islands	Sonora	Durango/ Sinaloa	Nayarit
Sonora	11			
Durango/Sinaloa	10	12		
Nayarit	5	12	7	
Jalisco	7	11	10	5

Glossophaga soricina leachii: Jones and Carter, 1976: 14. Name combination.

The subfamily Glossophaginae is represented on the islands by *Glossophaga soricina,* a species both widespread and common on the mainland. These small bats feed on nectar, pollen, and small fruits. Nelson (1899b) reported them feeding on the fruit of a wild fig (*Ficus* sp.). They are common on all four islands, although perhaps less so on San Juanito than on the others. The vegetation on San Juanito seems less favorable as a food source for nectarivorous bats. The first specimen from the islands was collected by Alphonse Forrer in 1881. Thomas (1881) uncharacteristically misidentified it as *Choeronycteris mexicana,* but subsequently corrected his mistake in a letter to C. Hart Merriam (Nelson, 1899b). That misidentification has persistently resurfaced in the literature on Mexican mammals. Although Tschudi (1844) listed the type locality only as Mexico in the original description of *Choeronycteris mexicana,* Elliot (1904) coined the common name "Tres Marías Islands bat" for this species, probably based on Thomas's mistaken report. Unfortunately, *Choeronycteris mexicana* has been listed from the Tres Marías in several recent compilations, based on Elliot's (1904) misconception (Hall and Kelson, 1959; Villa, 1967; Hall, 1981).

Nelson and Goldman found this species to be by far the most numerous bat on María Madre, and their series of 37 formed the basis of Merriam's (1898) description of *Glossophaga mutica.* Nelson (1899b: 18) described them as inhabiting ". . . every cave sufficiently deep to be dark." He specifically mentioned a cave formed in sea rocks near the settlement where *G. soricina* was common.

We found them equally common during our visit, including in what I assume to be the same cave described by Nelson. We even found them in a cave insufficiently deep to be dark, a small excavation at the base of a cliff that was purportedly used to house an occasional recalcitrant prisoner in solitary confinement. We also found them in a small concrete bunker, and collected several in mist nets set over small streams in arroyos. I shot a female with an attached young in a small crevice on San Juanito, and we netted one under a small fig tree near the base of a cliff. The only other evidence of reproductive activity was a single female with a 28-mm embryo. Nelson and Goldman found most females pregnant in May. The sex ratio was approximately equal in our samples.

These are small bats with an elongated rostrum, a conspicuously extensible tongue, a narrow uropatagium, and a small but discernible tail. The fur is pale basally and reddish brown distally. Forearm lengths range from 33 to 39 mm. The dental formula is I 2/2, C 1/1, P 2/3, M 3/3. The inner upper incisors are larger than the outer, and all are distinctly procumbent. The skull is somewhat slender, with the braincase longer than the rostrum but not conspicuously inflated.

The karyotype is $2n = 32$, $FN = 60$. The autosomal complement is a size-graded series of medium-sized to small metacentrics and submetacentrics. The X is a medium-sized submetacentric and the Y is a minute acrocentric (Baker, 1967).

The taxonomic and nomenclatural history of *Glossophaga* is convoluted (Gardner, 1986). Merriam (1898: 18) described *G. mutica* to differentiate it from mainland *G. soricina,* even though he stated: "In the absence of authentic skulls of *G. soricina* and *truei* for comparison, it is impossible to differentiate the cranial characters of *G. mutica.*" Miller (1913) reduced *mutica* to subspecific status under *soricina,* and recognized *G. s. leachii* as the mainland subspecies. Species limits and identities for mainland *Glossophaga* were confused until Webster and Jones (1980) clarified the situation by recognizing four sympatric species on the mainland. They argued persuasively that *Glossophaga leachii* is the correct name for what had been called *Glossophaga alticola,* and is not a junior synonym of *G. soricina.* They also studied my material from the Tres Marías Islands, along with the original series collected by Nelson and Goldman, and concluded that *mutica* differed significantly ($P \leq 0.5$) from mainland animals in forearm length, greatest length of skull, condylobasal length, length of rostrum, mastoid breadth, length of maxillary and mandibular toothrows, and length of mandible. As a result, they proposed the name *Glossophaga soricina handleyi* for the mainland populations.

TABLE 7
Measurements (in millimeters) of *Glossophaga soricina*

Variable	Tres Marías Islands (N = 20)		Probability	Mainland Nayarit (N = 91)	
	Mean ± SD	Range		Mean ± SD	Range
Total length	62.70 ± 4.99	57.00–80.00	NS	62.76 ± 4.18	52.00–72.00
Tail length	6.70 ± 1.03	5.00–9.00	<0.01	7.77 ± 1.34	4.00–10.00
Hind foot length	10.40 ± 1.35	8.00–12.00	NS	10.49 ± 0.84	7.00–12.00
Ear length	14.00 ± 0.76	12.00–15.00	NS	14.26 ± 1.30	12.00–19.00
Forearm length	36.92 ± 1.16	33.30–38.55	<0.001	35.82 ± 0.87	33.45–37.75
Greatest skull length	22.04 ± 0.34	21.40–22.70	<0.001	21.47 ± 0.34	20.75–22.30
Zygomatic breadth	9.39 ± 0.22	8.95–9.80	NS	9.40 ± 0.25	8.80–10.00
Mastoid breadth	9.10 ± 0.19	8.45–9.40	NS	9.04 ± 0.18	8.50–9.40
Condyloincisive length	20.74 ± 0.38	20.10–21.60	<0.001	20.21 ± 0.35	19.20–21.00
Postpalatal length	6.61 ± 0.27	6.00–7.00	<0.001	6.38 ± 0.21	5.90–6.95
Interorbital breadth	4.68 ± 0.13	4.45–5.10	NS	4.66 ± 0.13	4.30–4.95
Maxillary toothrow length	7.45 ± 0.26	6.65–7.85	<0.001	7.27 ± 0.18	6.85–7.75
Breadth across molars	5.50 ± 0.12	5.35–5.70	NS	5.53 ± 0.16	5.20–5.90

I analyzed 13 external and cranial characters on 20 specimens from the islands and 91 from the Nayarit mainland using both univariate and multivariate techniques (table 7). I can confirm the significant differences in forearm length, greatest length of skull, and length of maxillary toothrow noted by Webster and Jones (1980). Of the other characters mentioned by them, I looked only at mastoid breadth, which showed no significant difference in my analysis. I also found significant differences in tail length and in condyloincisive and postpalatal lengths. In general, *G. s. mutica* is larger than *G. s. handleyi* but has a shorter tail. A discriminant function analysis correctly classified 80 percent of the individuals.

SPECIMENS EXAMINED: María Cleofas Island, 5 (USNM); María Madre Island, 44 (USNM); María Magdalena Island, 9 (USNM); San Juanito Island, 3 (USNM).

Artibeus intermedius koopmani, new subspecies

Artibeus lituratus, Bogan, 1978. First record from Tres Marías Islands.

HOLOTYPE AND TYPE LOCALITY: The holotype, USNM 512378, is an adult male collected by Don E. Wilson (original number, 3678) on March 18, 1976, from María Cleofas, Tres Marías Islands, Nayarit, México. The specimen consists of a stuffed skin, cranium, and mandibles, all in good condition.

GEOGRAPHIC DISTRIBUTION: Known only from the Tres Marías Islands off the coast of Nayarit, México, where it occurs on all four islands: María Madre, María Magdalena, María Cleofas, and San Juanito.

ETYMOLOGY: I take great pleasure in naming this bat in honor of Dr. Karl F. Koopman, in recognition of his exceptional contributions to the field of bat systematics and zoogeography.

DIAGNOSIS: The following combination of characters sets *A. i. koopmani* apart from *A. i. intermedius* from the mainland: (1) averaging larger in total length, but with shorter feet, ears, and forearm; (2) generally darker both dorsally and ventrally, but with a distinct paler throat patch in most specimens; (3) skull longer and narrower (table 8); (4) upper incisors slightly prognathous, obviously extending anteriorly beyond the canines. Also, in most specimens, there are obvious gaps between the upper incisors, whereas in the nominate form the incisors usually are in contact.

DESCRIPTION: *Artibeus intermedius koopmani* is of medium size (forearm 58–68 mm) with grayish brown pelage. The head and body are covered by relatively long, thick fur. Over the back and rump, the hairs are about 8 mm long. Upperparts of head and body are gray-brown; individual hairs are tricolored—pale for approximately the basal 5 mm, followed by a 1–2-mm darker band, and many have a silvery tip. The silver tip is less conspicuous

TABLE 8
Measurements (in millimeters) of *Artibeus intermedius*

Variable	Tres Marías Islands (N = 107) Mean ± SD	Range	Probability	Mainland Nayarit (N = 112) Mean ± SD	Range
Total length	87.52 ± 3.80	77.00–95.00	<0.001	85.49 ± 4.84	72.00–95.00
Hind foot length	16.47 ± 0.97	14.00–20.00	<0.001	17.33 ± 1.85	12.00–21.00
Ear length	21.73 ± 0.81	20.00–24.00	<0.001	23.02 ± 1.62	19.00–26.00
Forearm length	63.29 ± 1.98	58.10–67.50	<0.001	64.28 ± 1.86	59.50–68.95
Greatest skull length	29.08 ± 0.64	27.55–30.65	NS	28.96 ± 0.56	27.45–30.25
Zygomatic breadth	17.73 ± 0.49	16.35–18.75	<0.001	18.20 ± 0.44	16.95–19.20
Mastoid breadth	15.79 ± 0.41	14.70–16.95	<0.001	15.99 ± 0.44	15.95–16.85
Condyloincisive length	25.79 ± 0.56	24.40–27.15	<0.05	25.61 ± 0.52	24.25–26.80
Postpalatal length	9.09 ± 0.31	8.15–9.80	NS	9.07 ± 0.38	8.05–9.95
Interorbital breadth	6.26 ± 0.24	5.80–7.10	<0.001	6.36 ± 0.23	5.80–7.05
Maxillary toothrow length	10.05 ± 0.25	9.35–10.70	NS	10.07 ± 0.25	9.50–10.70
Breadth across molars	12.30 ± 0.33	11.60–13.15	<0.001	12.51 ± 0.48	11.55–15.65

or missing on the nape, where the pale basal hairs show through. Similarly, on the throat, the hairs are almost unicolored, frequently giving the appearance of a pale throat patch. The demarcation between upperparts and underparts is inconspicuous. These are the largest bats on the islands and the most difficult to prepare as specimens because the skin adheres tightly to the pectoral muscles.

The ears are blackish brown and densely covered with short brown hairs only on the lower third. The tragus is about 5 mm long and bluntly rounded at the tip.

There is no tail. The uropatagium is roundly incised almost to the body in the midline and has long hairs, both dorsally and ventrally, that combine in many specimens to give the appearance of a fringe.

The hind feet are covered with brown fur. The plantar surface is much darker. The claws are dark basally but with unpigmented tips. The hind feet are relatively small for the body size.

The cranium is long and narrow, and generally resembles that of the nominate form. In dorsal view, the rostrum is moderately short and broad, the interorbital region narrow, and the braincase elongate. The braincase is convex in lateral view. The zygomatic arches are long and more widely expanded posteriorly across their squamosal roots than across the maxillary roots.

In lateral view, the nasals terminate anteriorly at a vertical line drawn between the premolars. The ventral maxillary roots of the zygoma arise at about the midpoint of the last molar. The auditory bullae are small and globular.

Short incisive foramina, long and broad palate, and small bullae are distinctive features visible in ventral view. The posterior margins of the wide incisive foramina lie just posterior to the canines. The broad palate extends 2 mm behind the last molars.

Each dentary is massive, averaging about 4 mm in depth immediately behind m3, and has a large coronoid process but reduced angular process. The posterior margin between the condyle and angular process is slightly concave.

The dental formula is I 2/2, C 1/1, P 2/2, M 2/3. The lower incisors are approximately equal in size and are crowded between the canines with no spaces between them. In unworn teeth, the anterior and occlusal surfaces are slightly concave, making the teeth appear weakly bifid. The canines are long and robust, with the cingulum expanded posteriorly into a shelflike projection.

The upper incisors extend anteriorly beyond the canines, and are distinctly bilobate. The cusps on the inner pair are scarcely subequal, with the inner one slightly longer. The outer pair is not bifid, but may appear so because the lower canines occlude against these teeth, leaving the anterior surfaces concave. The posterior surfaces of both pairs are concave in a dorsoventral direction.

The upper canines are long and robust, with relatively low cingula that terminate abruptly both posteriorly and anteriorly. On the lingual surface, the cingulum is somewhat expanded into a shelflike projection. The posterior margin of the canine is sharp, whereas the margin next to the incisors is rounded. In between, the lingual surface of the tooth is essentially flat.

The karyotype of *Artibeus intermedius* consists of 2n = 30 in females and 31 in males, owing to an XY_1Y_2 sex-determining system; FN = 56. There are seven metacentrics, three submetacentrics, and four subtelocentrics in the autosomal complement. The X is a large subtelocentric and both Ys are small acrocentrics (Baker, 1967).

Artibeus intermedius is the only stenodermatine on the islands. It is abundant on all islands, yet was not recorded by Nelson and Goldman (Nelson, 1899b). The Puritan expedition collected the species on María Magdalena and San Juanito, and we collected large series from the three larger islands and a few from San Juanito. We caught them in all habitats we sampled, and they were often the most common species at a given site. We did not find them roosting, and this perhaps accounts for them being overlooked by Nelson and Goldman.

Seventy percent of the animals we captured were males. Only 2 of 37 females were pregnant, both carrying 18-mm embryos.

In 1897 J. A. Allen described *A. intermedius* from two adults and five young from Costa Rica. He correctly diagnosed it as smaller and darker than *A. palmarum* (now considered a subspecies of *A. lituratus*), with narrower head stripes and obsolete cheek stripes. Andersen (1908) lumped *intermedius* with *palmarum* (which he placed as a subspecies of *A. jamaicensis*), and the name remained in synonymy until Goodwin (1969) resurrected it as the appropriate subspecies name for Mexican and Middle American populations of *A. lituratus*. Goodwin restricted *palmarum* to the population on Trinidad, but Davis (1984) elevated *A. intermedius* to specific status, and reinstated *palmarum* as the appropriate subspecific name for Middle American *A. lituratus*.

I assessed variation between the island population and that on the mainland by comparing 107 island animals with 112 from mainland Nayarit (table 8). In general, the island animals are larger in total length, but have smaller feet, ears, and forearms. The island animals have longer but narrower skulls. Student's *t*-tests revealed significant differences in 9 of the 12 characters studied. A discriminant function analysis correctly allocated 84 percent of the specimens.

SPECIMENS EXAMINED: María Cleofas Island, 57 (USNM); María Madre Island, 40 (USNM); María Magdalena Island, 24 (USNM), 2 (AMNH); San Juanito Island, 3 (USNM), 12 (AMNH).

Natalus stramineus mexicanus Miller

Natalus mexicanus Miller, 1902: 399. Type locality "Santa Anita, Lower California, Mexico."
Natalus stramineus mexicanus: Goodwin, 1959: 6. First use of current name combination.

In comparison to the limited number of species of frugivorous bats, more kinds of insectivores occur on the Tres Marías Islands. One that remains enigmatic is the funnel-eared bat, *Natalus stramineus*; only five specimens taken by the Puritan expedition on María Magdalena are known from the islands. We were unable to confirm the presence of *N. stramineus,* although we extensively mist-netted in appropriate locations. We did not locate caves on María Magdalena that would have been appropriate roosting sites. This species can be difficult to catch, so there is no way to know if they no longer occur there or if we simply were unable to capture them.

These bats are small, delicate in structure, and have large, funnel-shaped ears and tiny eyes. The fur is long and lax and is of one of two color morphs, a grey or a red that varies into shades of orange and yellow. The tail is enclosed in the rather substantial interfemoral membrane. The skull is also small and delicate, with an elongated rostrum and an abruptly rising braincase. The dental formula is I 2/3, C 1/1, P 3/3, M 3/3.

The karyotype is 2n = 36, FN = 56. There are 11 pairs of size-graded medium-sized to large biarmed and 6 pairs of acrocentric autosomes. The X is a small submetacentric and the Y is a small acrocentric (Baker, 1970).

Miller (1902: 399) named *Natalus mexi-*

canus to distinguish it from the South American *Natalus stramineus.* He recognized that it was closely related to *N. stramineus* even at the time: "In color as in other external characters *Natalus mexicanus* apparently does not differ from *N. stramineus.*" Subsequently, Dalquest and Hall (1949) named animals from the southern and more humid parts of the range *Natalus mexicanus saturatus.* They suggested intergradation in specimens from quite a broad range between the type locality of *mexicanus* in Baja California and that of *saturatus* in Veracruz, including Chihuahua, Sinaloa, and Morelos. Hall and Kelson (1959) extended the range of *N. mexicanus* south on the west coast of Mexico to Guerrero.

Goodwin (1959: 6–7) considered *N. mexicanus* and *N. stramineus* conspecific: "Because there appear to be no characters of specific rank that separate *mexicanus* from *stramineus,* and the actual differences are mainly in size, *mexicanus* is here recognized as a subspecies of *stramineus.*" He referred all specimens from localities south of Sinaloa to *saturatus,* even though a series from Amatlan, Nayarit, was paler in color than typical *saturatus* from Veracruz. Although Goodwin (1959: 7) continued to recognize *saturatus* as a subspecies distinct from *mexicanus,* he admitted: "There do not appear to be any actual characters separating *saturatus* from *mexicanus* except for an average difference in size, and even this character is not always consistent. . . . Additional material from Baja California may show that the relative difference in size between *N. s. mexicanus* and *N. s. saturatus* is even less than was originally supposed."

Although it is beyond the scope of this work, I do now have additional material from both Baja California and Nayarit to suggest that Goodwin was correct. The specimens from the Tres Marías Islands are also intermediate between the two subspecies and I suspect that eventually the two forms will be reunited under the older name *N. s. mexicanus.* Nevertheless, even if both forms continue to be recognized, I would be more inclined to refer the island specimens to *mexicanus*, simply because in color they resemble the paler forms of more arid regions to the north slightly more than the darker specimens from tropical areas.

SPECIMENS EXAMINED: María Magdalena Island, 5 (AMNH).

Myotis findleyi Bogan

Vespertilio nigricans: Thomas, 1881: 206. First record from Tres Marías Islands.
Myotis nigricans: Merriam, 1898: 18. Name combination.
Myotis californicus mexicanus: Miller and Allen, 1928: 160. Name combination.
Myotis findleyi Bogan, 1978. Type locality "Nayarit, Islas Tres Marias, Isla Maria Magdalena."

Alphonse Forrer took the first specimen, of which the skull at least is still in the British Museum (Bogan, 1978). Thomas (1881) identified it as the species we now know as *Myotis nigricans,* and noted that it represented a considerable range extension to the north. Nelson and Goldman failed to find them on the islands, and Nelson (1899b) subsequently speculated that the Forrer specimen represented only a straggler from the mainland. Miller and Allen (1928), in their revision of the American *Myotis,* allocated the Tres Marías specimen to *Myotis californicus* without comment. Subsequent workers followed that arrangement, and it remained for the Puritan expedition to verify their occurrence on the islands.

We found them on all three of the Marías and, although we did not take them there, I suspect that they occur on San Juanito as well. Bogan (1978) studied our large series from the islands, and compared them with mainland populations of *M. nigricans, M. californicus, M. leibii,* and *M. carteri.* As a result, he named *Myotis findleyi* as a distinct species.

The specimens obtained by the Puritan expedition were taken by knocking them down with branches as they came to drink over a small arroyo. Our specimens were all taken in mist nets set in similar situations. The family Vespertilionidae is the most diverse on the islands, with four species. Along with *Natalus,* this richness suggests that on the islands fruit and flowers are less predictable resources than insects.

None of our specimens showed overt signs of reproductive activity, which probably indicates that they breed slightly later in the year.

Although obviously related to *M. carteri,* the mainland counterpart, these are distinctive bats. The pelage is long and the hair is bicolored, dark basally with paler, almost buffy tips. All study skins have a characteristic rumpled appearance. These are very small bats, significantly smaller than *M. carteri* in most measurements (Bogan, 1978). The dental formula is I 2/3, C 1/1, P 3/3, M 3/3.

SPECIMENS EXAMINED: María Cleofas Island, 6 (USNM); María Madre Island, 1 (USNM); María Magdalena Island, 20 (USNM), 8 (AMNH).

Lasiurus blossevillii teliotis (H. Allen)

Atalapha noveboracensis frantzii: Thomas, 1881: 205. First record from Tres Marías Islands.

Atalapha teliotis H. Allen 1891: 5. Type locality "unknown, but it is probably southern California."

Lasiurus borealis mexicana: Merriam, 1898: 19. Name combination.

Lasiurus blossevillii teliotis: Baker et al., 1988: 9. First use of current name combination.

As with many other species, the first specimen from the islands was collected by Alphonse Forrer for the British Museum. Thomas (1881) correctly identified it at the time, and subsequently Allen proposed the name *Atalapha teliotis* for populations from western North America. Nelson and Goldman did not find this species during their visit to the islands, and Nelson (1899b) suggested that they were there only as stragglers from the mainland. They were taken again by the Puritan expedition on María Magdalena. We found them common on all three of the larger islands.

Most of our specimens were netted over small pools in arroyos. This species was one of the earlier flyers, and frequently could be seen before dark. We shot a few as they foraged low over the canopy along the edge of a small stream on María Cleofas. Strangely, most of our specimens were males, including all 15 from María Magdalena, 38 of 39 from María Madre, and 9 of 16 from María Cleofas. None of the females showed any sign of reproductive activity.

Red bats are strikingly colored animals. The dorsal hairs have three, and in some females four, bands of contrasting color. The bases are black, and the midregion of each hair is pale buff. Many of the hairs are then tipped distally with various shades of red and orange. Some females have an additional band of silvery frosting at the tips of some hairs. These are arranged in irregular bands across the dorsum, resulting in a slightly hoary pattern. The interfemoral membrane is covered with red or orange hair dorsally, which frequently extends to the trailing edge of the membrane. The skull is short and broad. The dental formula is I 1/3, C 1/1, P 2/2, M 3/3.

The karyotype is 2n = 28, FN = 48. Autosomes consist of seven pairs of large metacentrics, three pairs of medium-sized metacentrics, one pair of small metacentrics, and two pairs of small acrocentrics. The X is a medium-sized submetacentric and the Y is an acrocentric (Baker and Mascarello, 1969).

Western red bats were long thought to represent a well-marked subspecies of *Lasiurus borealis* of eastern North America. Baker et al. (1988) argued for specific distinctness between eastern and western red bats based on the results of studies using starch-gel electrophoresis. The oldest available name for this group is *Lasiurus blossevillii,* formerly considered a South American subspecies of *L. borealis.*

I assessed geographic variation between samples representing the islands and mainland Nayarit by comparing 13 characters in 56 specimens from the islands and 5 from the mainland. Island bats average slightly larger in most characters, significantly so in zygomatic and mastoid breadth (table 9). Externally, they are roughly the same size, except for strikingly smaller hind feet in the island animals. No island specimens had hind feet longer than 8 mm and no mainland specimens measured less than 8 mm. A discriminant function analysis correctly allocated 100% of the specimens.

In addition to the quantitative differences, there are visible differences between pelages of the two populations. The island animals have pelage that appears paler overall because of the tendency of the pale buff band to be slightly broader. The red tips are grouped into lines that tend to be slightly farther apart, and the terminal frosting is missing or only barely apparent, even in females.

TABLE 9
Measurements (in millimeters) of *Lasiurus blossevillii teliotis*

Variable	Tres Marías Islands (N = 56) Mean ± SD	Range	Probability	Mainland Nayarit (N = 5) Mean ± SD	Range
Total length	102.16 ± 4.08	95.00–112.00	NS	103.00 ± 3.87	98.00–107.00
Tail length	41.79 ± 2.90	36.00–50.00	NS	41.20 ± 2.86	37.00–45.00
Hind foot length	6.61 ± 0.56	5.00–8.00	<0.001	8.80 ± 0.84	8.00–10.00
Ear length	11.13 ± 0.74	9.00–13.00	NS	11.60 ± 0.89	10.00–12.00
Forearm length	38.86 ± 1.09	36.20–42.25	NS	39.80 ± 1.49	37.90–41.90
Greatest skull length	11.89 ± 0.24	11.50–12.55	NS	11.77 ± 0.19	11.45–11.90
Zygomatic breadth	9.09 ± 0.22	8.70–9.65	<0.05	8.88 ± 0.21	8.60–9.65
Mastoid breadth	7.68 ± 0.17	7.35–8.00	<0.05	7.50 ± 0.14	7.30–7.65
Condyloincisive length	12.57 ± 0.24	12.20–13.30	NS	12.40 ± 0.16	12.20–12.60
Postpalatal length	5.52 ± 0.17	5.15–5.85	NS	5.44 ± 0.10	5.30–5.55
Interorbital breadth	4.34 ± 0.10	4.05–4.55	NS	4.35 ± 0.14	4.25–4.55
Maxillary toothrow length	4.18 ± 0.10	4.00–4.45	NS	4.23 ± 0.14	4.05–4.40
Breadth across molars	5.80 ± 0.15	5.60–6.20	NS	5.78 ± 0.23	5.55–6.15

SPECIMENS EXAMINED: María Cleofas Island, 16 (USNM); María Madre Island, 39 (USNM); María Magdalena Island, 15 (USNM), 2 (AMNH).

Rhogeessa parvula parvula H. Allen

Rhogeessa parvula H. Allen, 1866: 285. Type locality "Tres Marías, Mexico."
Vesperugo parvulus: Thomas, 1881: 203. First record from Tres Marías Islands.

Colonel Andrew Jackson Grayson obtained the first specimens of this species in 1865, later described as *Rhogeessa parvula* by Allen (1866). Alphonse Forrer subsequently collected a specimen for the British Museum in 1881. Nelson and Goldman killed two that were flying along a trail in brilliant sunshine in the middle of the forenoon. This species was also collected by the Puritan expedition. We found them common on all four islands.

These little bats are not only common, but are unusually visible because they tend to fly early in the afternoon, well before dusk in many cases. They were seen foraging in the forest in the late afternoon and were active just before and after dusk near all of our campsites. Their high visibility probably is the reason they were obtained much earlier than some of the other bats now known from the islands.

Rhogeessa parvula is the smallest bat on the islands. The fur is pale fawn-colored at the bases, but the color darkens to a chestnut brown on the tips. The upper side of the uropatagium is well furred to about midtibia. The skull is tiny, with an unusually narrow postorbital region. The dental formula is I 1/3, C 1/1, P 1/2, M 3/3.

The karyotype is 2n = 44, FN = 50. The autosomal complement consists of 1 pair of large metacentrics, 1 pair of medium-sized metacentrics, 1 pair of small metacentrics, 1 pair of medium-sized subtelocentrics, and 17 pairs of medium-sized to small acrocentrics. The X is a medium-sized subtelocentric and the Y is a small submetacentric (Baker and Patton, 1967).

I assessed geographic variation in 13 characters by comparing 9 specimens from the islands with 49 from mainland Nayarit. The island specimens are smaller in all measurements, significantly so in 10 of the 13 (table 10). The skulls are consistently narrower in island animals, especially in the mastoid area, where no island skulls measure over 6.5 mm and no mainland specimens measure less than 6.5 mm. A discriminant function analysis correctly allocated 100% of the specimens.

I believe that the differences between the island and mainland populations are sufficiently trenchant to warrant subspecific recognition. *Rhogeessa parvula* was considered

TABLE 10
Measurements (in millimeters) of *Rhogeessa parvula*

Variable	Tres Marías Islands (N = 9)			Mainland Nayarit (N = 49)	
	Mean ± SD	Range	Probability	Mean ± SD	Range
Total length	68.89 ± 3.62	61.00–73.00	<0.001	73.02 ± 2.47	69.00–79.00
Tail length	26.11 ± 2.62	21.00–30.00	<0.01	30.12 ± 2.06	26.00–32.00
Hind foot length	4.44 ± 0.53	4.00–5.00	<0.001	6.16 ± 0.62	4.00–7.00
Ear length	11.89 ± 0.60	11.00–13.00	NS	12.73 ± 1.38	11.00–14.00
Forearm length	27.75 ± 0.76	26.20–28.65	NS	28.34 ± 0.80	26.45–29.75
Greatest skull length	11.89 ± 0.24	11.45–12.10	<0.001	12.30 ± 0.26	11.90–12.65
Zygomatic breadth	7.54 ± 0.27	7.10–7.95	<0.001	7.95 ± 0.20	7.55–8.40
Mastoid breadth	6.35 ± 0.13	6.10–6.50	<0.001	6.67 ± 0.13	6.50–6.95
Condyloincisive length	11.24 ± 0.24	10.80–11.55	<0.001	11.58 ± 0.23	11.15–12.05
Postpalatal length	4.41 ± 0.10	4.20–4.55	NS	4.38 ± 0.16	4.00–4.65
Interorbital breadth	2.95 ± 0.09	2.85–3.10	<0.001	3.12 ± 0.12	2.90–3.40
Maxillary toothrow length	4.21 ± 0.11	4.10–4.35	<0.001	4.38 ± 0.11	4.10–4.60
Breadth across molars	4.84 ± 0.18	4.55–5.15	<0.001	5.08 ± 0.17	4.90–5.65

monotypic from 1866 until 1958, when Goodwin (1958) recognized five subspecies ranging from Sonora, Mexico, to Ecuador. LaVal (1973) elevated one of these, *R. minutilla,* to specific status, and placed three others, *aeneus, io,* and *velilla,* in the synonymy of *R. tumida,* returning *R. parvula* to monotypic status. LaVal (1973) also placed *R. tumida major,* a subspecies described by Goodwin (1958), in the synonymy of *R. parvula.* Consequently, *Rhogeessa parvula major* Goodwin, with type locality of "San Bartolo Yautepec, Yautepec, Oaxaca, Mexico," is available and should be used for the mainland populations.

The pattern of geographic variation within mainland populations was though by LaVal (1973) to be essentially clinal, with animals increasing in size from north to south. However, a close examination of his data shows that the smallest animals occur in Nayarit, with size increasing both to the north and to the south. Additional study of these mainland populations may well reveal that a northern subspecies should be recognized as distinct from the nominate form on the Tres Marías Islands and from *R. p. major* in the south.

SPECIMENS EXAMINED: María Cleofas Island, 1 (USNM); María Madre Island, 9 (USNM), 2 (AMNH); María Magdalena Island, 2 (USNM), 5 (AMNH); San Juanito Island, 1 (USNM).

Bauerus dubiaquercus Van Gelder

Antrozous (Bauerus) dubiaquercus Van Gelder, 1959: 2. Type locality "María Magdalena Island, Tres Marías Islands, Nayarit, Mexico."
Bauerus dubiaquercus: White, 1969: 277. First use of current name combination.

The first specimens were collected by the Puritan expedition in 1957. The bats were captured by knocking them down with branches as they flew over a small stream. We found them common in similar habitats on all three of the large islands. It seems unusual that this large, distinctive species remained undetected by early collectors, although it is fairly inconspicuous. These bats do not fly early in the evening, and we only found them foraging or coming to drink over forest streams.

These bats are unique among North American vespertilionids in having large ears and dark brown coloration (fig. 12). Although most closely related to *Antrozous pallidus,* they are readily distinguished by the darker coloration and slightly shorter and narrower ears. The skull has a pronounced sagittal crest, relatively small auditory bullae, an anteriorly convergent upper toothrow, and the talonid of the third lower molar approximately equal in length to the trigonid. A spiculelike third lower incisor is present in most specimens.

The karyotype is 2n = 42, FN = 52. The autosomal complement is composed of 2 pairs

Fig. 12. *Bauerus dubiaquercus* from the Tres Marías.

of large, 1 pair of medium-sized, and 2 pairs of small metacentrics, and a graded series of 16 pairs of medium-sized to small acrocentrics. The X is a medium-sized submetacentric and the Y is a small acrocentric (Engstrom and Wilson, 1981).

Although this uncommon species was not known to science until 1959, it has since been taken from several localities on the mainland (Engstrom et al., 1987). Pine (1966) described a specimen from Veracruz as *Baeodon meyeri.* White (1969) elevated *Bauerus* to generic status based on his studies of fossil nyctophiline bats from California. Pine et al. (1971) recorded two specimens from Honduras as *Antrozous* (*Bauerus*) *dubiaquercus meyeri.* Engstrom and Wilson (1981) added another specimen from Veracruz, and extended the mainland range much closer to the Tres Marías with a specimen from Jalisco. Dinerstein (1985) extended the range south to Costa Rica. During a joint UNAM–USNM expedition to Chiapas in 1982 we collected a single individual in a mist net over a small river (Medellin et al., 1986). McCarthy (1987) added two specimens from Belize.

Engstrom and Wilson (1981) reviewed geographic variation within this species based on examination of pelage and multivariate analyses of external and cranial measurements of 29 specimens from the Tres Marías and 5 specimens from the mainland. They regarded the species as monotypic because there was as much variation among mainland specimens as is found between the nominal island form and the proposed mainland subspecies *B. d. meyeri.* They also recommended that because differentiation between *Bauerus* and *Antrozous* equals that found among most genera of vespertilionid bats, *Bauerus* should be accorded generic rank, as had been done earlier by White (1969).

SPECIMENS EXAMINED: María Cleofas Island, 18 (USNM); María Madre Island, 6 (USNM); María Magdalena Island, 18 (USNM), 4 (AMNH), 1 (UNAM).

Sylvilagus graysoni (J. A. Allen)

Lepus graysoni J. A. Allen, 1877: 347. Type locality "Tres Marias Islands, Nayarit, Mexico" ("undoubtedly from Maria Madre" [Nelson, 1899b: 16]).

Sylvilagus (*Sylvilagus*) *graysoni:* Lyon, 1904: 336. First use of current name combination.
Sylvilagus graysoni badistes Diersing and Wilson, 1980: 15. Type locality "San Juanito Island of the Tres Marias Islands, Nayarit, Mexico."

Dampier (1729) mentioned that "*Indian* conies" were plentiful on the Tres Marías, presumably referring to this species. Grayson collected the first cottontails from the islands in 1865 and sent them to the American Museum of Natural History, where J. A. Allen named them after him. Alphonse Forrer also obtained two specimens for the British Museum in 1881. In 1897, Nelson and Goldman found this species abundant in some places on San Juanito, María Madre, and María Magdalena, and said that it was reported to occur on María Cleofas as well. They found them to be numerous around a deserted ranch on María Magdalena, but rather scarce elsewhere on that island. They also reported them to be extraordinarily abundant and surprisingly tame in old fields around an abandoned ranch on María Madre. They killed some with stones, and suggested that they could have collected over a hundred in a morning, should they have wished to do so. The animals sat quietly in the bushes until driven out into the open, where they would remain until a camera was brought up and focussed within quite close range. Nelson and Goldman found them to be much less numerous in forested areas. Additional specimens were obtained by the California Academy of Sciences expedition in 1925 (McClellan, 1926), and sometime during the 1960s by field parties from the University of British Columbia.

These are medium-sized to large rabbits with relatively short ears. They are reddish-colored dorsally, with the nape and rump the brightest. Laterally, they are paler reddish, and the venter is whitish except for the brownish throat patch. The skull is also medium-sized to large, with a long rostrum, long diastema, and long incisive foramina. The maxillary toothrow is relatively short, and the basioccipital is narrow.

The karyotype consists of a 2n of 42 and an FN of 78. The autosomal complement includes 15 pairs of medium-sized to small meta- and submetacentrics and 5 pairs of small acrocentrics or subtelocentrics. Some of these latter five pairs may bear satellites on the short arms. The X chromosome is a small acrocentric or subtelocentric and the Y is a very small acrocentric (Diersing and Wilson, 1980).

We found these rabbits abundant only on San Juanito, where their behavior was much as had been described by Nelson (1899b). They still occur on the other islands, but not in large numbers. Nelson (1899b) also noted the extreme fragility of the skin of these rabbits, a character we can confirm after preparing study skins. The extreme tameness of the rabbits may be due to a dearth of predators. Nelson (1899b) suggested that raccoons, red-tailed hawks, and caracaras were probably their only predators.

We found 2 females carrying 75-mm embryos, and 11 were lactating during our visit in March.

Diersing and Wilson (1980) documented distribution patterns of the four species of *Sylvilagus* known from west-central México. They revised the taxonomy of those species, including *S. graysoni.* Their results suggested that *S. graysoni* is most closely related to *S. cunicularius* of the nearby mainland, and that the ancestral stock of *S. graysoni* may have reached the islands during some earlier period of land connection to the islands. After becoming established on all four islands, the population on San Juanito must have become isolated from the others, as that population is distinct enough to warrant subspecific recognition as *S. g. badistes.*

SPECIMENS EXAMINED: María Cleofas Island, 1 (USNM); María Madre Island, 22 (USNM), 2 (AMNH), 2 (CAS); María Magdalena Island, 4 (USNM), 1 (AMNH), 1 (UBC), 7 (UMMZ); San Juanito Island, 13 (USNM), 6 (AMNH).

Peromyscus madrensis Merriam

Peromyscus madrensis Merriam, 1898: 16. Type locality: "Maria Madre Island, Tres Marias Islands, Mexico."
Peromyscus boylei madrensis: Osgood, 1909: 152. Name combination.
Peromyscus boylii madrensis: Miller and Kellogg, 1955: 495. Name combination.

When Alphonse Forrer visited the Tres Marías in 1881, he found that the inhabitants knew of no rats or mice whatever in the islands, except for *Rattus rattus,* which obviously reached there considerably earlier. This

information seems to be due to few local inhabitants, rather than to a lack of native mice. Nelson and Goldman obtained the first specimens of the Tres Marías deer mouse in 1897. They suggested that the species was the most widely distributed and the most numerous rodent on the islands. They found them on the three large islands, but doubted their existence on San Juanito, where land crabs are numerous. In contrast, we found them abundant on San Juanito, María Madre, and María Cleofas, but absent from María Magdalena.

On María Cleofas, *P. madrensis* was abundant in a variety of habitats. They were common in the forests above the shoreline and also in shrubby areas near shore. They were also abundant in an arroyo containing a freshwater stream. They live under logs and projecting roots, as well as under rocks and small ledges. We found one lactating female and one with three 20-mm embryos. Fourteen males had scrotal testes in March.

Although Nelson and Goldman found them on María Magdalena in 1897, we were unsuccessful in collecting them there despite intensive efforts. We suspect that their absence is due to the presence of one or more of three exotics that have since been introduced to María Magdalena. *Rattus rattus* was known only on María Madre at the time of Nelson and Goldman's visit (Nelson, 1899b). We found them throughout María Magdalena, even near the center, at an elevation of 500 m. In contrast, we found no *R. rattus* on María Cleofas, where the *Peromyscus* population is thriving. On María Madre,we found *Peromyscus* only away from human habitations, where *R. rattus* was common. Domestic goats and white-tailed deer (*Odocoileus virginianus*) also have been introduced to María Magdalena, and have drastically altered the undergrowth.

This is a relatively large member of the *Peromyscus boylii* species group, with a long, indistinctly bicolored tail, the terminal third of which is as dark below as above. It has large hind feet and relatively short ears. The skull is comparatively large, but with relatively short toothrows and small auditory bullae. The dentition is relatively simple (Carleton et al., 1982).

The karyotype is 2n = 48, FN = 54. The autosomal complement comprises 1 pair of large subtelocentrics, 1 pair of medium-sized subtelocentrics, 2 pairs of small submetacentrics, and a graded series of 19 pairs of large to small acrocentrics. The X is a large subtelocentric and the Y is a small subtelocentric (Carleton et al., 1982).

Merriam (1898) suggested that *P. madrensis* was most closely related to *P. spicelegus* on the mainland, and Osgood (1909) arranged both as subspecies of *P. boylii.* Carleton (1977) reinstated *madrensis* as a full species and questioned its relations to both *boylii* and *spicelegus.* Carleton et al. (1982) used our newly collected material to demonstrate that the closest mainland relative of *P. madrensis* is likely *P. simulus,* based on a variety of morphological characters and zoogeographic relations. Interestingly, their multivariate analyses revealed taxonomic differences separating populations on María Cleofas, María Madre, and San Juanito, exceeding any recorded between mainland samples of *P. boylii, P. simulus,* or *P. spicelegus.* This is similar to the situation found among populations of *Sylvilagus* by Diersing and Wilson (1980).

SPECIMENS EXAMINED: María Cleofas Island, 42 (USNM); María Madre Island, 26 (USNM); María Magdalena Island, 1 (USNM); San Juanito Island, 24 (USNM), 2 (AMNH).

Oryzomys nelsoni Merriam

Oryzomys nelsoni Merriam, 1898: 15. Type locality "María Madre Island, Tres Marías Islands, Mexico."

The Tres Marías rice rat is an enigmatic species. Four specimens were taken by Nelson and Goldman in 1897 and described as new by Merriam the following year. They found them only in a limited area of small springs near the summit of María Madre. In 1976, we located the area, locally known as "Sacatal" because of the unusually lush growth of grass, and found only *Rattus rattus* there. The species is most likely extinct, having been displaced by *R. rattus.*

Oryzomys nelsoni was a large rice rat with the tail much longer than the head and body. The upperparts are a rich ochraceous-buffy color that is most intense on the rump. The head, shoulders, and lower parts of the sides are paler, although the face, top of the head, and back have some dusky hairs as well. The

underparts are white, and the ears are thinly covered with grayish hairs. The tail is pale brown above and below near the tip, but yellowish underneath near the base. The skull is long and narrow, but massive. The rostrum is heavy and strongly decurved.

This species seems most closely allied to *Oryzomys couesi* of the mainland, but with only four specimens it is difficult to establish exact relationships. Goldman (1918), the last revisor of the genus, hypothesized that it was closest to *O. couesi,* but commented on its striking difference from all mainland forms in the remarkable development of the rostrum.

SPECIMENS EXAMINED: María Madre Island, 4 (USNM).

Rattus rattus (Linnaeus)

[*Mus*] *rattus* Linnaeus, 1758: 61. Type locality "Europaea," subsequently fixed as "Sweden (Uppsala)" by Thomas (1911).

Mus decumanus: Thomas, 1881: 212. First record from the Tres Marías Islands.

Rattus rattus: McClellan, 1926: 321. First use of current name combination for Tres Marías Islands specimens.

Black rats were likely introduced to María Madre early, as it was a popular stop for Spanish explorers and buccaneers (Dampier, 1729). Thomas (1881: 212) said: "According to Mr. Forrer . . . it appears, however, that the inhabitants know of no rats or mice whatever in the islands, except, of course, the cosmopolitan *Mus decumanus,* Pall." As all subsequent specimens have been of black, rather than Norway, rats, I assume that the inhabitants simply had the local rats misidentified.

We found *R. rattus* abundant and widespread on María Madre and María Magdalena. As mentioned in the accounts of the native rodents, I strongly suspect that *Rattus* has caused the extinction of *O. nelsoni* and has sharply reduced the populations of *P. madrensis.* These animals are highly adaptable and provide formidable competition for native rodents everywhere, but especially in insular situations like the Tres Marías. We did not find them on María Cleofas or San Juanito, but their introduction to those islands is probably just a matter of time.

SPECIMENS EXAMINED: María Madre Island, 32 (USNM); María Magdalena Island, 13 (USNM).

Stenella longirostris (Gray)

Delphinus longirostris Gray, 1828. Type locality unknown ("Cape Good Hope" [True, 1889: 76]; "not Cape of Good Hope as ordinarily cited" [Miller and Kellogg, 1955]).

Prodelphinus longirostris: Merriam, 1898. First record for Tres Marías Islands.

Stenella longirostris: Iredale and Troughton, 1934. First use of current name combination.

Stenella microps: Miller and Kellogg, 1955. Name combination.

Spinner dolphins were first collected from the Tres Marías Islands by Nelson and Goldman (Nelson, 1899b). They reported them in schools of 100–200 individuals in the waters between the islands and the mainland. Goldman shot two but one sank, so there is only a single specimen (Nelson, 1899b). There is also a specimen at the California Academy of Sciences collected in 1919 (J. G. Mead, personal commun.).

According to Nelson (1899b), this species appears slimmer and more graceful in the water than the more common porpoise in the area, *Tursiops truncatus.* The large groups seen by Nelson and Goldman were frequently accompanied by swarms of seabirds. On one occasion, a large group attended by a shrieking crowd of seabirds passed under and on all sides of their boat, breaking the water into foam (Nelson, 1899b).

We did not encounter such large groups in 1976, when Robert L. Brownell recorded observations of all marine mammals. *Stenella longirostris* was seen only twice; on 16 March at 0730 hours an unknown number were seen 6 miles southeast of María Cleofas, and a single individual was seen on 23 March at 1000 hours 1 mile southeast of San Juanito.

The taxonomy of *S. longirostris* was reviewed by Perrin (1975a, 1975b). Although he did not formally recognize subspecies, these animals would be referred to his subsp. B, which he called the eastern Pacific spinner porpoise. Perrin (1975a) pointed out several problems in the nomenclature of this species, and provisionally dated the name from

Schlegel (1841) because the holotype of *S. longirostris* (Gray, 1828) may have been lost. In the same year (1975b), Perrin recommended dating the name from Gray (1828) in the interest of stability, and because the potential problem was, in all likelihood, unresolvable.

SPECIMENS EXAMINED: 12–15 miles off Tres Marías Islands, 1 (USNM).

Stenella attenuata (Gray)

Steno attenuatus Gray, 1846: 44. Type locality unknown.
Stenella attenuata: Iredale and Troughton, 1934: 66. First use of current name combination.
Stenella graffmani: Van Gelder, 1960: 15. First record from Tres Marías Islands.

I am aware of only a single specimen of spotted dolphin from the Tres Marías, a skull picked up on the beach of María Magdalena by the Puritan expedition (Van Gelder, 1960). We recorded them four times during our trip in 1976. At 0715 hours on 6 March, 10–12 were seen about 10 miles off María Magdalena; at 1800 hours on 10 March, 6–8 were seen 2 miles off the southeast end of María Madre; at 1025 hours on 13 March, 30–40 were seen 8 miles southeast of María Cleofas; and at 1435 hours on 13 March, 10 were seen about 48 miles southeast of María Cleofas.

An excellent summary of the nomenclature of this species was provided by Perrin et al. (1987). Although here I follow their usage of *S. attenuata* for this species, it seems to me that the correct name is *Stenella velox.*

SPECIMENS EXAMINED: María Magdalena, 1 (AMNH).

Tursiops truncatus aduncus (Ehrenberg)

Delphinus aduncus Ehrenberg, 1832: 1 (footnote). Type locality Belhosse Island, Red Sea.
? *Phocaena communis:* Merriam, 1898: 19. First record for Tres Marías Islands.
Tursiops nuuanu: Van Gelder, 1960: 17. Name combination.
Tursiops truncatus aduncus: Hershkovitz, 1966: 48. First use of current name combination.

Nelson (1899b: 19) said: "Porpoises supposed to belong to this species were common around the shores of the Tres Marias and also in bays and mouths of streams or lagoons along the coast of the mainland. They were always seen in the belt of shallow discolored water within a short distance of the shore. As soon as blue water, with a depth of over 40 fathoms, was reached, the other porpoise (*Prodelphinus longirostris*) was encountered. The common porpoise was seen in schools of 10 to 30 or 40 individuals swimming in loose order. At Maria Madre they came into the shallow bay in front of the settlement in the early morning and followed close along shore." The animals they saw must have been *Tursiops truncatus* rather than *Phocaena phocaena,* a species not known south of the United States in the eastern Pacific. Brownell (1983, 1986) presented considerable evidence to show that neither *P. phocaena* nor *P. sinus* is known from the waters near the Tres Marías Islands.

Bottlenosed dolphins were first collected from the Tres Marías Islands by the Puritan expedition in 1957. They harpooned one individual and picked up a partial skull from the beach. The harpooned individual was among a group of about 50 swimming slowly along the shore in a cove on the southeast end of San Juanito.

We found this species to be the most common cetacean in the waters around the islands. Our records include 2 seen at 1130 hours on 7 March off the southeast end of San Juanito, 8–10 seen at 1215 hours on 7 March off the north end of San Juanito, 3 seen at 1502 hours on 7 March off the northwest end of María Madre, 5 seen at 1510 hours off the northwest end of María Madre, about 40 seen at 1025 hours on 9 March about 1.5 miles off María Cleofas, 5 seen at 1530 hours on 12 March ¾ mile off northeast end of María Magdalena, 1 seen on 17 March off the northeast end of María Magdalena, and 1 seen on 22 March between María Madre and San Juanito.

SPECIMENS EXAMINED: María Magdalena, 1 (AMNH); San Juanito, 1 (AMNH).

Megaptera novaeangliae (Borowski)

Balaena Novae Angliae Borowski, 1781: 21. Type locality "an den küsten von Neuengland."
Megaptera novaeangliae: Kellogg, 1932: 148. First use of current name combination.

The Puritan expedition photographed humpback whales off the Tres Marías and reported them as common around the islands (Van Gelder, 1960). Four animals were definitely identified as humpbacks, and several others were too far away for accurate identification. Traveling between the Tres Marías and Isla Isabela, ". . . at least one spout could be seen on the horizon at any time" during the early afternoon (Van Gelder, 1960: 10).

In discussing the main wintering grounds of humpback whales, Rice (1974: 185) included: "The mainland coast of west-central Mexico, from southern Sinaloa to Jalisco, especially in the vicinity of the Islas Tres Marías and Isla Isabela, Nayarit, and Bahía Banderas, Jalisco." Urbán and Aguayo (1987) confirmed this as a major wintering subregion, and suggested that it must have been so for at least the past 100 years. We found them in all of these places during March 1976.

Our Tres Marías observations include 1 seen on 7 March at 0900 hours just off the main village of Puerto Balleto on María Madre, 2 or 3 seen on 9 March at 0937 hours off the north end of María Cleofas, 2 seen on 10 March at 1435 hours in the channel between María Cleofas and María Magdalena, 2 seen on 10 march at 1520 hours in the channel between María Cleofas and María Magdalena, 1 seen on 10 March at 1550 hours in the channel between María Cleofas and María Magdalena, 3 seen on 12 March at 1413 hours about 1½ miles off Salinas on María Madre, and 1 seen on 12 March at 1550 hours several miles off the northeast end of María Magdalena.

Although we saw no other baleen whales during the trip, several other species may occur in these waters. Van Gelder (1960) saw whales between María Cleofas and María Magdalena that he tentatively identified as finbacks (*Balaenoptera physalus*). Rice (1974) saw a blue whale (*Balaenoptera musculus*) midway between Cabo San Lucas and the Tres Marías in 1967. He also saw Bryde's whales (*Balaenoptera edeni*) in the area, and commented that "The floating factories that operated on the west coast of Mexico in 1913/14, 1924/25 to 1928/29, and 1935 reported taking 121 'sei' whales between Bahía San Juanico, Baja California, and the Islas Tres Marías, Nayarit. Because sei whales are scarce in this area, whereas Bryde's whales are common, I believe that most if not all of the animals reported as 'sei' whales were probably Bryde's whales."

Zalophus californianus (Lesson)

Otaria californiana Lesson, 1828: 420. Type locality San Francisco Bay, California.

Zalophus californianus: J. A. Allen, 1880: 276. First use of current name combination.

That seals or sea lions occurred on the Tres Marías Islands at times in the past seems beyond doubt. Because no specimens are known from there, the identification is less certain, but *Zalophus californianus* seems the most likely candidate. Dampier (1729: 191) said: "The Sea is also pretty well stored with Fish, and Turtle or Tortoise, and Seal. This is the second Place on this Coast where I did see any Seal. . . ." Allen (1880) supposed these "seals" to have been the California sea lion, but observed that they may have been the northern elephant seal, although in that case Dampier would probably have alluded to their greater size.

A large seal or sea lion, called "lobo marino" by the Mexicans, was reported to occur on the rocky shores of María Magdalena and María Cleofas when Nelson and Goldman visited in 1897 (Merriam, 1898; Nelson, 1899b). They had reports of them even before leaving San Blas on the Nayarit mainland. Apparently they had been hunted for sport by various visitors until they had become scarce. Nelson and Goldman made special efforts to find them, and accompanied a local guide to both islands. They saw only a single seal, on a rocky islet off the shore of María Cleofas, and it escaped into the water before they could fire a shot. The consensus among the locals was that the seals were scarce at that time, only a remnant of the considerable number that once lived there. Nelson's notes suggest: "They are doubtless doomed to speedy extinction" (Merriam, 1898: 18).

By the time of the visit of the Puritan expedition in 1957, long-time residents had never seen, heard, or heard of sea lions around the Tres Marías (Van Gelder, 1960). Likewise, we found no knowledge of sea lions when we visited in 1976. Gallo and Ortega (1986) recently recorded the first sea lion from

the Mexican mainland at Acapulco, so animals once again may populate the Tres Marías.

Procyon insularis Merriam

Procyon cancrivorous: Thomas, 1881: 208. Not *P. cancrivorous* Cuvier. First record from the Tres Marías Islands.

Procyon lotor insularis Merriam, 1898: 17. Type locality "María Madre Island, Tres Marías Islands, Mexico."

Procyon insularis insularis: Nelson and Goldman, 1931: 20. First use of current name combination.

Procyon insularis vicinus Nelson and Goldman, 1931: 20. Type locality "Maria Magdalena Island, Tres Marias Islands, off coast of state of Nayarit, western Mexico (altitude 250 feet)."

The first mention of raccoons on the Tres Marías was by Dampier (1729), who reported them as plentiful. Grayson (1871) mentioned seeing raccoons on the islands, but failed to secure specimens. Alphonse Forrer collected one for the British Museum, subsequently misidentified by Thomas (1881) as *P. cancrivorous.* Nelson and Goldman collected six from María Madre and two from María Magdalena in 1897, subsequently described as a new subspecies of the widespread *P. lotor* of the mainland by Merriam (1898). The Puritan expedition secured an additional six from María Madre in 1957.

We were unable to secure specimens of this species, but we did see tracks on María Madre. We also saw a captive individual in the village on María Madre. We found no sign of them on the other islands, and it is possible that they no longer occur on María Magdalena.

Procyon insularis is a large, pale raccoon with relatively short, rather coarse pelage. The upperparts are generally pale creamy buff, but thinly overlaid with black. The nuchal patch is at best only faintly differentiated by a pale buffy line. The sides are paler and without the black-tipped hairs. The top of the head is grizzled gray and black and the black mask extends across the face from the nasal pad to the middle of the forehead. The underparts are pale brown basally, overlaid with pale creamy buff. The skull is large, angular, and massive, with heavy zygomata. The postorbital processes are well developed.

Merriam (1898: 14) clearly considered this species to be simply a well-marked insular variant of *P. lotor,* but indicated that "Those who insist on intergradation as the touchstone of subspecies will have to set it up as a full species." Nelson and Goldman (1931), who collected the series on which Merriam based the description, apparently thought it deserved full specific rank when they described *Procyon insularis vicinus* based on the two specimens from María Magdalena as a subspecies distinct from *P. i. insularis* from María Madre. Curiously enough, later in the description they referred to these subspecies as "*P. l. insularis*" and "*P. l. vicinus*" instead of *P. i. insularis and P. i. vicinus* (Nelson and Goldman, 1931: 21). Although this might be an indication of some equivocation on their part, it was likely a lapsus, because Goldman (1950) in his subsequent revision of *Procyon* left no doubt that he regarded them to represent subspecies of *P. insularis,* a species he considered distinct from *P. lotor.*

Although the differentiation of subspecies on such closely adjacent islands seems strange, it parallels the situation we subsequently found in *Sylvilagus* (Diersing and Wilson, 1980).

SPECIMENS EXAMINED: María Madre Island, 6 (USNM), 6 (AMNH); María Magdalena Island, 2 (USNM).

Odocoileus virginianus sinaloae J. A. Allen

Odocoileus sinaloae J. A. Allen, 1903: 613. Type locality "Escuinapa, southern Sinaloa, Mexico."

Odocoileus virginianus sinaloae: Lydekker, 1915: 159. First use of current name combination.

Both white-tailed deer and domestic goats were introduced to María Magdalena in 1903 (Hanna, 1926). At the time of the California Academy of Sciences Expedition in 1925, the local inhabitants reported that populations of both had increased, but neither was seen by members of the expedition. W. H. Burt collected two specimens in 1938, apparently the first taken from the island population. By 1955, when an ornithological expedition from the Los Angeles County Museum visited the island, both species were common (Stager, 1957). The Puritan expedition obtained three specimens in 1957.

Fig. 13. *Odocoileus virginianus sinaloae* from María Magdalena.

At the time of our visit in 1976, both deer and goats were common enough on the island to have created a distinct browse line on the trees in some areas. We collected two specimens of deer, bringing the total known from this introduced population to seven.

The pelage is short and coarse, ranging from dark brown to light tawny dorsally and almost white ventrally (fig. 13). These deer are quite small for the species in general, but slightly larger than *O. v. acapulcensis* from Colima. They do not differ in any appreciable way from *O. v. sinaloae* from the mainland.

SPECIMENS EXAMINED: María Magdalena Island, 2 (USNM), 3 (AMNH), 2 (UMMZ).

DISCUSSION

Taxonomic allocation of insular populations has long been nonplussing. There are alternative extreme points of view, both of which have their adherents among systematic zoologists. The physical isolation provided by islands certainly decreases or eliminates gene flow between populations, and it can be argued that any corresponding morphological differentiation deserves taxonomic recognition. Strict adherence to this point of view might lead to recognition of insular subspecies whose degree of differentiation is less than that found among mainland populations. Some insular endemics might not be accorded full specific rank if they also occurred on the mainland.

A case can also be made for simply describing the differentiation of insular populations without according them taxonomic recognition. Ideally, one should have a full understanding of the amount and kind of geographic variation throughout the range of a species in order to properly judge the significance of variation between an insular and corresponding mainland population. This is more likely to be the case in revisionary works that it is in faunal surveys.

Examples abound in the mammalogical literature of insular populations being treated as identical to mainland subspecies, endemic

subspecies, endemic species, and even endemic polytypic species. Populations of *Didelphis marsupialis* on Coiba and San Miguel islands off the coast of Panama are each recognized as separate subspecies, whereas populations of *Didelphis virginiana* on Cozumel Island off the coast of Mexico are considered the same as the mainland subspecies (Hall, 1981; but see also Gardner, 1973). Similarly, shrews of the *Sorex cinereus* group on islands off the coast of Alaska have been considered the same as wide-ranging mainland forms (Nunivak Island), as insular subspecies (St. Lawrence Island), and as endemic species (Pribilof Islands), as well as all simply being described as similar tundra forms (Hoffmann and Peterson, 1967; Van Zyll de Jong, 1976). On Caribbean islands, bats of the genus *Pteronotus,* subgenus *Chilonycteris,* are closely related to the widespread polytypic species *P. personatus.* They have differentiated sufficiently to be recognized as two separate polytypic species, each of which has separate subspecies on Cuba and Jamaica (Smith, 1972; Silva, 1979).

All of these alternative relationships can be found in the Tres Marías Islands. Four species of bats—*Macrotus waterhousii bulleri, Natalus stramineus mexicanus, Lasiurus blossevillii teliotis,* and *Bauerus dubiaquercus*—are best considered to represent the same taxa as mainland forms. Each of these does differ from mainland forms in some characters, and revisionary studies based on specimens from throughout the range of a species might alter the current arrangement. This is particularly true for *Bauerus dubiaquercus,* currently known from few specimens over a wide area of the mainland.

The marsupial (*Marmosa canescens insularis*) and three species of bats (*Glossophaga soricina mutica, Artibeus intermedius koopmani,* and *Rhogeessa parvula parvula*) represent subspecies endemic to the islands. Each clearly represents an insular population of a wide-ranging mainland species that can be distinguished statistically by a variety of characters.

The two rodents (*Peromyscus madrensis* and *Oryzomys nelsoni*) and one bat (*Myotis findleyi*) are currently considered to represent species distinct from close mainland relatives. The relationships of *Oryzomys nelsoni,* known from only a few specimens, and now almost certainly extinct, remain unresolvable. *Myotis findleyi,* although closely related to *Myotis carteri* on the mainland, is as distinctive as many currently recognized species in that genus. Systematic relationships within the genus *Myotis* warrant further study, and it is possible that *Myotis findleyi* and *Myotis carteri* will eventually be considered conspecific. *Peromyscus madrensis* is distinct, with less clear-cut mainland relatives, although Carleton et al. (1982) presented cogent arguments for closest relationship with *P. simulus* of the mainland.

Finally, the two largest native mammals of the islands, *Sylvilagus graysoni* and *Procyon lotor,* are considered not only specifically distinct from mainland forms, but have differentiated between islands. In both cases, the differences, although subtle, are of the same order of magnitude as those used to distinguish subspecies elsewhere.

The high degree of endemism in the mammal fauna is not matched by the other terrestrial vertebrates. The avifauna was thoroughly analyzed by Grant (1965), who used a strict 90% criterion to demonstrate that 20 of the 34 land bird species represented endemic subspecies. None was judged sufficiently distinct to warrant specific recognition. The herpetofauna is even less well differentiated, with only 2 of 20 species represented by endemic subspecies. There is also an endemic genus of snakes (*Exelencophis nelsoni*), but it is known from a single specimen, now lost, and Zweifel (1960) was dubious that it represented even an endemic species, instead of an endemic genus.

The biogeographic relations of the mammal fauna of the Tres Marías lie with the nearest mainland areas of Nayarit and Jalisco. In general, the fauna comprises a group of species whose closest mainland relatives are distributed through the subtropical parts of Mexico, rather than the more arid areas to the north, or the central plateau. Also, there is no evidence suggesting a link with Baja California.

Two species that have differentiated among the islands are the largest members of the native fauna, *Procyon insularis* and *Sylvilagus graysoni.* The degree of differentiation they reflect suggests long residency. Perhaps they became established early, when the area was much closer to the mainland. The other

three small terrestrial mammals—*Peromyscus madrensis, Oryzomys nelsoni,* and *Marmosa canescens*—clearly have differentiated from their mainland counterparts. They are likely candidates for rafting to the islands on debris coming out of the larger mainland rivers, perhaps at a time when the water barrier was narrower and shallower than now. The bats are much more mobile and are susceptible to long-distance transport by storms. Several have differentiated sufficiently to suggest that they were early colonizers of the islands.

Distribution patterns within the islands seem clearly related to island size. María Madre, the largest, has (or had) 12 of the 13 native species known from the islands. The only species not known from there is *Natalus stramineus,* a bat known from the islands only from five specimens collected in 1957. We were unable to verify its occurrence in 1976. *Oryzomys nelsoni,* the rice rat known only from four specimens collected in 1897, is likely extinct.

María Magdalena, the next largest island, has (or had) 11 and possibly 12 of the 13 known native species. There are no specimens of *Marmosa canescens,* but local inhabitants reported them to Nelson and Goldman in 1897. We were unable to verify the occurrence of *Peromyscus madrensis* there in 1976, and the thriving population of *Rattus rattus* on María Magdalena may have led to the extirpation of the native mouse.

María Cleofas has 9 of the 13 native species, and it is possible that one of the bats that we did not find there, *Macrotus waterhousii,* will eventually be collected there. The best remaining undisturbed habitats are on María Cleofas, making it an ideal candidate for a reserve to protect the unique fauna of the islands.

The smallest island, San Juanito, also has the fewest species, 6 of the 13. It is possible that some additional species of bats will eventually be collected there.

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Tent Construction and Use by *Uroderma bilobatum* in Coconut Palms (*Cocos nucifera*) in Costa Rica

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ABSTRACT

Tent construction and use, uniformity of tents, and frond selection were studied in a population of *Uroderma bilobatum* roosting in coconut palms (*Cocos nucifera*) in Guanacaste Province of northwestern Costa Rica during July 1988. Palm leaflets were cut at their midribs in a line converging distally with the frond midrib, and the leaflets collapsed downward to form a large enclosed tent. Tent height, number of leaflets cut, and angle between the line of cut leaflets and the midrib of the fronds were measured to assess uniformity of tent construction. To ascertain if bats were selecting specific trees or fronds, we measured the angle of orientation of cut fronds, number of fronds hanging above a tent, and tree height. Bat tents were found in palms with a narrower range of heights than the overall tree population, and trees with tents were taller on average than trees without tents. A single altered frond provides excellent protection from rainfall. Bats do not seem to prefer fronds based on number of overhanging fronds or angle of orientation. The age of the modified frond may be an important factor in roost site selection, as tents in younger fronds were more likely to be occupied than those in older fronds. The number of bats roosting under tents ranged from 1 to 15 adults and subadults. The colony was composed largely of adult females and two age classes of young.

INTRODUCTION

It has been known for over half a century that some bats create their own roosting sites by modifying the shapes of leaves (Barbour, 1932; Chapman, 1932). Bats create these structures by severing the veins and, in some cases, the interconnecting tissues of leaves of various species. The sides of the leaves then collapse downward along the midrib to form a dark, secluded roosting site for the bats. Because some styles of these modified leaves are pyramidal or "tent-shaped," all modified leaves are now called bat tents and the bats that modify them are called tent-making bats.

Fourteen species of New World phyllostomid bats, all in the subfamily Stenodermatinae, are known to construct tents (Timm, 1987). Additionally, two Old World species of flying foxes—*Cynopterus brachyotis* and *C. sphinx* (family Pteropodidae)—have been reported to modify palms to produce diurnal roosting structures (Phillips, 1924; Goodwin, 1979). Reviews of tent construction and use by bats were provided by Kunz (1982) and Timm (1987).

In Costa Rica and elsewhere in the Neotropics we have found that (1) tent bats are often highly localized in occurrence; (2) tent bats seem to be most concentrated in areas that have an abundant supply of the preferred plant species used in tent construction; (3) quite often tents are concentrated in localized areas even though the preferred plant species is more widely distributed; (4) the location of tents within plants varies, as does the shape

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of tents constructed by a given species of bat; and (5) there are often many more tents present in an area than are occupied by bats. These factors suggest that the bats are selecting specific leaves for tents and using only certain tents of those available on a daily basis. Roost site selection in tent bats has been investigated previously for only a few species of the smaller tent-makers: *Artibeus phaeotis* (Timm, 1987), *Artibeus watsoni* (Choe and Timm, 1985), *Ectophylla alba* (Timm and Mortimer, 1976; Brooke, 1990), and *Vampyressa nymphaea* (Brooke, 1987). These studies concluded that bats select specific species of plants for tent construction and that they often select specific ages of leaves. Because of the large size of many altered leaves, especially those of pinnately compound plants, a considerable amount of energy probably is expended by the bat or bats in creating these roost sites. The energetic costs associated with the elaborate nature of many styles of bat tents, especially those constructed by bats of the genus *Uroderma,* suggest that strong selection pressures are involved.

Interestingly, no studies have addressed roost site selection and tent use by Peters's tent-making bat (*Uroderma bilobatum*), the first species of Neotropical bat discovered to modify leaves and one of the largest and most widely distributed of the Neotropical tent-making bats. Our discovery of a sizable population of *U. bilobatum* in the Pacific lowlands of Costa Rica roosting in altered fronds of coconut palms provided an ideal opportunity to explore several aspects of tent construction and use by these bats. The goals of this study were to (1) determine whether *U. bilobatum* chooses specific trees or fronds for tent construction, (2) assess whether they construct tents of a uniform shape or height, (3) determine if tents are effective protection from rain, and (4) evaluate patterns of tent use (including group size, group composition, and movement between tents).

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METHODS

From 16 through 21 July 1988, individuals and groups of *Uroderma bilobatum convexum* and their tents in coconut palms (*Cocos nucifera*) were observed. The planted coconut grove contained 56 trees that varied in height and age, and was located approximately 0.5 km east of the administrative buildings at Refugio Nacional de Fauna Silvestre Dr. Rafael Lucas Rodríguez Caballero (commonly known as Palo Verde) in the Pacific lowlands of northwestern Costa Rica. Palo Verde is a wildlife refuge located approximately 2 km south and 12 km east of Bolsón in Guanacaste Province (10°30′N, 85°20′W; elev. 10 m). The area lies within the Tropical Dry Forest Life Zone (Holdridge, 1967) and is dominated by lowland deciduous and riverine swamp forests and a large seasonal marsh. Rainfall is extremely seasonal, with most of the mean annual precipitation of 1700+ mm falling between April and October. Details of the vegetation, habitat types, and climate of Palo Verde have been described by Slud (1980) and Hartshorn (1983).

All bat tents were surveyed daily, and the number of roosting bats present in each tent was counted. Nursing, nonvolant juvenile offspring (forearm = 32.5 mm [N = 1]) were clearly visible clinging to 23 adult females (forearm $\bar{x}$ = 42.5 mm [N = 2]), enabling us to easily distinguish them from other bats.

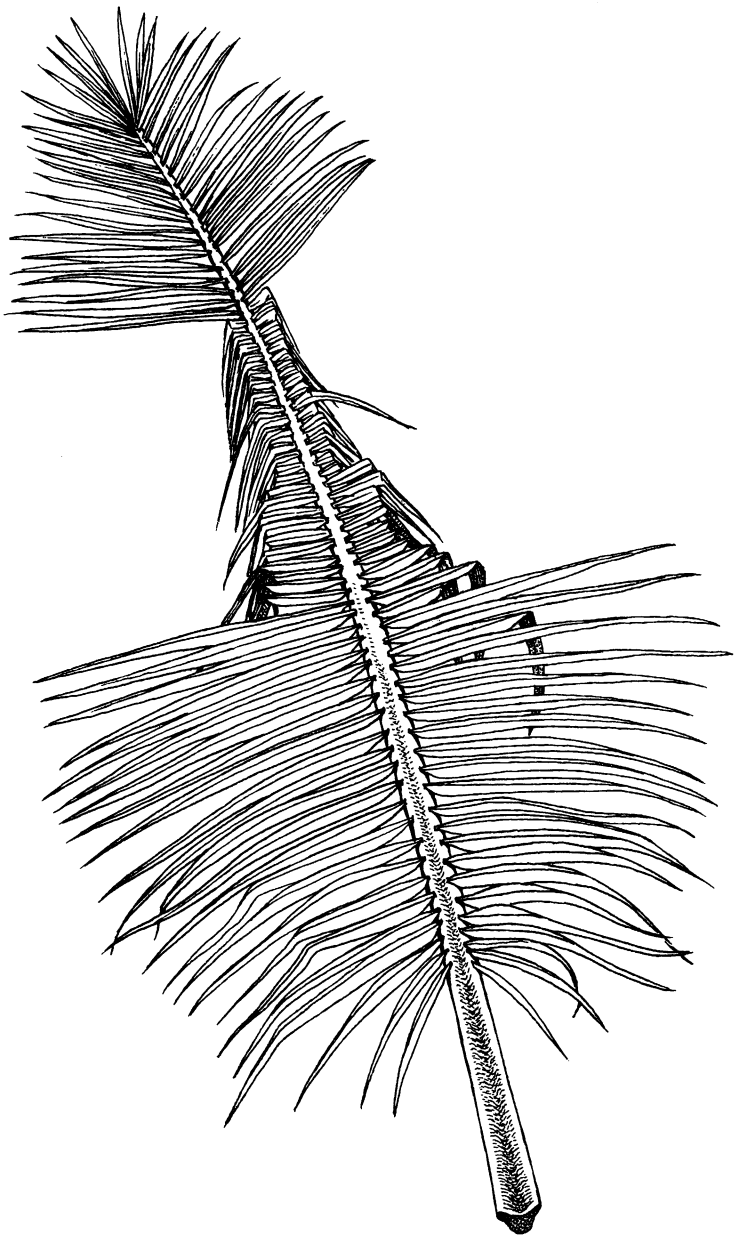

Fig. 1. Dorsal view of a coconut frond showing the leaflets cut by *Uroderma bilobatum* to form a tent.

Twenty-three of the 41 adult and subadult bats present were captured in mist nets, and 21 of these were marked for future identification. Volant bats were judged to be adults if the phalangeal epiphyses were fused, and subadults if the epiphyses were not yet fused.

To test whether *Uroderma* selects specific trees or fronds for tent construction, the following measurements were taken. We measured the distance from the ground to the point where the lowest green frond attached to the tree (to the nearest 0.1 m). This provided an estimate of tree height, because coconut trees shed the lowest leaves as they

grow taller and leaves are concentrated at the very top of the tree. To assess whether bats were selecting fronds with respect to the direction the fronds hung, we measured the compass direction of each cut frond to the nearest degree. The number of fronds directly above a tent was counted to determine if bats were constructing tents in fronds that had fronds above, possibly providing additional shade or protection from rain.

Two aspects of the coconut trees and altered fronds were measured to assess the degree of uniformity among tents in this area. First, leaflets hanging perpendicularly to the plane of the frond up to the point where the line of cuts converged with the midrib of the frond were counted as cut leaflets that contribute to the tent; any cut leaflets distal to the point of convergence with the midrib were not counted (fig. 1). Second, the angle between the midrib and one of the two rows of cut leaflets was estimated (with a protractor) to the nearest degree.

We also assessed protection from rainfall under tents by measuring water collected over a 4-day period in a 250-ml beaker placed directly under the center of a typical tent, in the position bats normally hang. During the same period, two additional beakers were placed in the open to measure total rainfall.

To evaluate patterns of tent use, we surveyed group size and composition under individual tents throughout the study. Two factors—age of fronds and tent height—were examined to ascertain if bats occupied specific tents of the total tents available. The age of the cut frond (young or old) was estimated by the frond's position on the tree in relation to other fronds. Tent height was measured (to the nearest 0.1 m) as the distance from the ground to the point at which the line of cut leaflets converged with the frond midrib.

A reference specimen of *Uroderma bilobatum* from this population was deposited in the Museo Nacional de Costa Rica in San José; the museum's mammals recently were transferred to INBio (the new National Biodiversity Institute, Santo Domingo, Costa Rica).

RESULTS

At Palo Verde, *Uroderma bilobatum* severs the midrib of leaflets on the large, pinnately compound-leafed coconut palm, *Cocos nucifera,* to form dark, secluded diurnal roosts and maternity sites. The cut leaflets fold downward, perpendicular to the ground, creating large, angular tents (fig. 2). Bats cut the midrib of leaflets but do not appear to sever surrounding tissue, nor do they sever the midrib of the frond. The leaflets closest to the tree trunk are severed at the greatest distance from the midrib of the frond. This distance decreases as the cuts proceed distally to a point at which they converge with the frond midrib (fig. 1). A variable number of leaflets beyond the point of convergence may also be cut. Tent shape is a combination of the number of leaflets cut and the angle at which the line of cuts is made.

Of the 56 trees in the coconut grove, 23 contained tents constructed by *U. bilobatum.* Forty-four tents were located on our first survey. Three additional tents were constructed over the next five nights. Of those trees that had tents, the mean number of tents per tree was 2.0 (range 1–5, SD = 1.2). The road and trails within a 1.5-km radius of the study site were searched for additional tents or large-leafed trees appropriate for tents, but none were found.

Of all the trees in the grove, the range of heights of trees with tents encompassed the taller trees, but excluded the very tallest. The average height of the lowest green frond (our estimate of tree height) of all trees was 1.8 m (range 0.5–5.4 m, SD = 0.96). Bat tents were found in trees that averaged 2.3 m in height to the lowest frond (range 1.6–3.0 m, SD = 0.42). The average height of trees with tents (2.3 m, N = 23) was higher than the average for trees without tents (1.5 m, N = 33, range 0.5–5.4 m, SD = 1.08; Wilcoxon rank sum, $P < 0.001$).

The orientation of the frond and the number of fronds above a tent did not affect which fronds the bats selected for tent construction. There was no pattern to the orientation of cut fronds; the compass direction ranged from 0 to 352° ($\bar{x} = 191°$, SD = 101°). The number of fronds above a given tent ranged from 0 to 3 ($\bar{x} = 0.7$, SD = 0.85).

Although there was a definite inverted V-shaped pattern to the general form of tents constructed, actual tent shape was variable. Of 26 tents we were able to measure and count, 17 had leaflets cut on both sides and

Fig. 2. Tent of *Uroderma bilobatum* in the pinnately leafed coconut palm *Cocos nucifera.*

9 had leaflets cut on only one side. The mean number of leaflets cut per side was 12.8 (range 0–36, SD = 7.9). The angle formed by the frond midrib and the line of cut leaflets averaged 32.3° (range 20–46°, SD = 7.7°).

Two beakers placed in the open each collected approximately 90 ml of rainfall during a 4-day period. The beaker placed under a bat tent during the same period collected only 2 ml of rain.

Although 44–47 tents (3 tents were constructed during our study) were available to the roosting bats, only 9–11 were occupied on any given day during the study. Sixty-nine percent of the occupied tents were in use 4 or more days. Thirty-four tents were never occupied during the study. Occupied tents appeared to be spatially clumped within the coconut grove.

Occupied and unoccupied tents differed in frond age and height. Occupied tents tended to be in younger fronds (fronds higher in the tree) than did unoccupied tents ($\chi^2 = 10.9$, $P < 0.05$). Sixty-seven percent of occupied tents

were found in young fronds, whereas 84 percent of unoccupied tents were in old fronds. Accordingly, tent height differed significantly between occupied ($\bar{x}$ = 4.6 m, SD = 0.8) and unoccupied tents ($\bar{x}$ = 3.8 m, SD = 0.7 m; Wilcoxon rank sum = 2.3, $P < 0.05$).

Fourteen trees had two or more tents, but in only one instance was more than one tent occupied in a single tree. That tree had five tents, one of which was occupied on 5 of the 6 days by a large cluster of bats. On one of those days, an additional tent was occupied by a single bat. The other three tents in this tree were never occupied.

On three occasions we observed *U. bilobatum* roosting under coconut fronds that clearly had not been altered to form a tent. The leaflets of each of these fronds drooped naturally perpendicular to the ground, similar to the pattern seen in cut leaflets. Two of these fronds were occupied by single bats for 1 day only. The third was used by three, two, and four bats on consecutive days.

Of the 13 different tents used by bats (and 3 unaltered fronds), 8 were occupied by single bats and 8 by groups of two or more bats. The average group size was 5.2 (range 1–15, SD = 3.3). Twenty-three of the 34 groups (68%) were composed primarily of females with nursing offspring.

Forty-one adult or volant subadult *U. bilobatum* were observed in the coconut grove on the first day, and of these 23 were adult females that had nutritionally dependent, juvenile offspring. We captured 16 adult females, 1 adult male, 5 subadult males, and 1 subadult female. Fourteen of the adult females were lactating, one was visibly pregnant, and one was postlactating. Six females were captured while carrying their offspring within the first 30 minutes after sunset. Females that were lactating but not carrying their offspring were captured later in the evening. The single adult male observed had fully scrotal testes. No other species of bats were found roosting under the coconut fronds.

Over the 6-day period when bats were marked, the lactating females with nursing young roosted in six of the tents (table 1). Not all of these six tents were continuously occupied over the 6-day period. Of our 28 observations of tents occupied by lactating females, on 10 occasions the groups included only the mother/offspring pair(s) and on 18 occasions included mother/offspring pair(s) and 1–9 ($\bar{x}$ = 1.9) other nonlactating bats. On three occasions we observed single, lactating females roosting alone with their offspring. Each of these females roosted in a different tent, and each mother/offspring pair was found alone only for 1 day. Three of the marked subadults roosted singly, one roosted with an adult female and her offspring, one roosted with one to three other bats, and one roosted in a large cluster of bats that included lactating adult females and their nursing offspring.

TABLE 1

Distribution and Numbers of *Uroderma bilobatum* Roosting in 13 Tents and 3 Unaltered Fronds (indicated by *) in Coconut Palms (*Cocos nucifera*) at Palo Verde in 1988[a]

Tent no.	16 July	17 July	18 July	19 July	20 July	21 July
1	15/6	13/10	9/6	3/3	0	1/1
2	6/5	4/4	8/8	7/6	10/7	9/6
3	6/5	6/5	6/5	5/4	5/4	5/4
4	7/7	4/4	0	3/3	1/1	4
5	1	2/2	2/1	2/1	2/1	2/1
6	0	2	3	4	3	4
7	1	2	1	1	1	1
8	1	1	1	1	1	1
9	1	1	1	1	0	0
10	1	1	0	0	1	1
11	1	0	0	0	0	0
12	1	0	0	0	0	0
13	0	0	0	0	1	1
14*	0	0	1	3	3/1	1/1
15*	0	2	0	0	0	0
16*	0	0	0	0	0	1

[a] The numerator (or single number in a column) is the number of adults and/or volant subadults; the denominator is the number of juveniles (nonvolant) observed. 0 = no bats present in tent that day.

DISCUSSION

The species of bats that use modified leaves as diurnal roost sites face both advantages and disadvantages due to this roosting strategy. Potential advantages of roosting in tents include the ability to change roost sites as food availability or weather conditions change

or as ectoparasite infestations increase, as well as protection from predators that specialize on more traditional bat roosts such as caves or hollow trees. Disadvantages include the energetic costs of modifying the leaf; the ephemerality of the leaf, causing the need for construction of new roosts every few months; vulnerability of bats roosting under leaves to rain, heat, and wind; and vulnerability to certain arboreal predators. Depending on the habitat, suitable roost sites may or may not be readily available. These and other costs and benefits are likely to affect roost site selection by tent-making bats.

At Palo Verde, *Uroderma bilobatum* constructs tents in coconut palms by partially cutting leaflets along a line tapering distally toward the midrib (fig. 1). The pattern of leaf modification is similar to that in tents cut by *U. bilobatum* in the palm *Scheelea rostrata,* as well as in a variety of other large-leafed plants (Timm, 1987). Both the angular cut and the selection of large-leafed plants seem characteristic of this species. Although the inverted V-shaped tent style is characteristic and easily recognizable, we observed considerable variability among individual tents. Some tents were cut only on one side, varying numbers of leaflets were cut, and the angle at which the line of cut leaflets converged toward the midrib varied.

The most important factor we studied regarding frond selection for tent construction was the height of the tree. Bats construct tents in trees in only a narrow range of the total available tree heights. Trees taller than average, but not the tallest, are used. Taller trees may provide increased protection from climbing predators, but very tall trees may be more exposed to high-velocity wind. Bats did not select fronds on the basis of their angle of orientation or on whether or not the frond was overhung by one or more other fronds.

At first glance, pinnately compound palm leaves, with their gaps between leaflets, might not seem to provide adequate protection from the torrential rain showers of the lowland tropics. However, the results of our simple test, measuring rainfall under a tent versus in the open, strongly suggest that tents provide roosting bats with excellent protection from rain. During our study, 90 ml of rain fell in this area, but the beaker placed under a bat tent in the position where bats roost collected only 2 ml of water.

Age of the frond may also be an important factor in the selection of a specific tent as a roost site. Tents in younger fronds are more likely to be occupied than those in older fronds. It is likely that tents in more mature fronds represent older, previously occupied tents constructed when the leaf was younger. Young fronds are more tender and probably easier to modify than older fronds. Tents constructed in young fronds will be available as roosting sites for a longer period of time than those in older fronds. Younger fronds are farther from the ground and may be more difficult for predators to reach. These young fronds also have more pliable rachises, which may provide a more "sensitive" early warning of the approach of a climbing predator. Because fronds are present on coconut trees for 2.5–3 years (Vandermeer, 1983), tents constructed in these fronds are potentially available to bats for many months. As tents age, they are increasingly damaged by wind and other environmental factors and become less suitable as roost sites. While this provides a partial explanation for the observation that there were many more tents in the area than were in use at any one time, extra tents may also provide an alternate roost site for bats that have been disturbed in their tents. We observed single bats flying from one tent to another during our census on three occasions; these were bats that we accidentally disturbed.

Tents in general, as well as occupied tents, appeared to be clumped within the coconut grove. This clumped distribution could be due to the social organization of the bats, but more likely is due to the clumped distribution of preferred trees. Taller trees tended to be clumped in this area. The relative importance of these factors could best be studied in an area where tree heights are randomly distributed or where palms are all of equal height.

The range of *Uroderma bilobatum* extends throughout Central America and northern South America, and the bats are found in a variety of habitats. In tropical dry forests such as at Palo Verde, bats seem to be limited in

available roost sites because the large-leafed plants they prefer are uncommon or absent. A search of the trails at the wildlife refuge produced no plants that seemed suitable for tent construction by this species, other than the planted coconut palms. This suggests that the bats may be locally limited by the number of available roost sites. However, the number of bats roosting in the coconut grove diminished throughout the 6 days of our study, perhaps because they were sensitive to our disturbance, so alternative roost sites may be available in the area.

Bats roosted alone or in groups of up to 15 adults or subadults in the coconut grove. Females with nursing young were most likely to be found with at least one other bat (other than their offspring), and most groups were composed of lactating females. Maternity roost formation is a common phenomenon in many species of bats. It seems likely that during the period of parturition and lactation, the tents in this area are used by *Uroderma bilobatum* as maternity roosts. The dynamics of maternity roost formation and group composition will be addressed in a future paper. Our observations of females with nutritionally dependent juveniles and volant subadults that appeared to be of uniform age support the classification of *U. bilobatum* as being bimodally polyestrous, as suggested by previous studies of this species (Fleming et al., 1972; Wilson, 1979; Baker, 1981; Baker and Clark, 1987).

Our observations, and those of previous workers (summarized by Timm, 1987), show that groups of *Uroderma bilobatum* roost under leaves that have been altered by the bats to form tents. *Uroderma* selects large leaves that may be in a variety of shapes; however, the tents constructed are characteristically created with a large, inverted V-shaped pattern in the cut leaf or leaflets. Considerable energy is expended by the bats to create these roosts, as evidenced by the large size of the cut area made by *Uroderma* and by our observations that a period of several nights is required for the creation of a new tent. Lactating females at Palo Verde usually roosted in groups containing more than one bat. Volant, nonreproductive subadults may roost singly or with groups of adult females. Tent roosts provide the bats with excellent protection from rain. Although tents probably require considerable effort to construct, in coconut palms they remain available to the bats for a period of at least several months, providing the bats with protection from the elements and undoubtedly from predators as well.

ADDENDUM

Lewis returned to Palo Verde during June and July of 1989 and surveyed the numbers of *Uroderma bilobatum* roosting under the fronds of this same grove of coconut palms as part of a study on the population dynamics of these bats. She found 54 tents in 26 of the 54 coconut trees in the area. In early June, from 6 to 10 *U. bilobatum* were using the palm tents. As the study progressed, the greatest number of bats observed roosting in the palm grove on one day was 35. Both male and female bats were observed roosting under tents.

During early February 1990, Kathryn E. Stoner visited Palo Verde and surveyed the numbers of *U. bilobatum* for us at this same grove. Of the 42 tallest trees in the coconut grove, 21 contained one or more tents. The bat tents were checked for occupancy during four consecutive days. On 2 February, three bats were observed in this grove, each roosting singly under tents in separate trees. On 3 February, two bats were observed roosting together in a fourth tent in another tree (fig. 3); no other bats were observed. On 4 February, there were no bats roosting under any of the tents. On 5 February, only one bat was found; it was roosting under the same tent that contained two bats on 3 February.

On 2 February 1991, Timm returned to this site to survey the numbers of *U. bilobatum* in this coconut grove. He found a total of 41 tents in 29 of the 54 trees. Only three *U. bilobatum* were found, each roosting singly under fronds that had been altered to form tents.

These additional observations emphasize the flexibility of tent-making bats regarding roost sites. *U. bilobatum* appears to use this grove seasonally. It is possible that some bats move into or out of the area to track changing food resources (Kunz, 1982); movement back to the grove might revolve around colonial

Fig. 3. Two *Uroderma bilobatum* roosting in a coconut palm tent. Photograph courtesy of Kathryn E. Stoner.

maternity roosting and/or mating. Additional research, especially following marked bats throughout the year, would be extremely valuable in determining the factors affecting movements and choice of roosts by these bats.

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A Fossil *Myospalax* Cranium (Rodentia: Muridae) from Shanxi, China, with Observations on Zokor Relationships

MARIE A. LAWRENCE[1]

ABSTRACT

A fossil myospalacine cranium is described and provisionally referred to *Myospalax youngi*. An analysis of 40 character states is provided and a hypothesis of the phylogeny of fossil and Recent myospalacine rodents is presented. All myospalacines, fossil and Recent, are assigned to the genus *Myospalax* Laxmann, 1769, as they represent a monophyletic group derived from primitive muroids. Some areas for further study are discussed.

INTRODUCTION

Myospalacine rodents—zokors—are fossorial muroids with a Recent distribution in northern China, southern Mongolia, and Manchuria as well as in western Siberia. These rodents were first introduced to European zoologists by Riech Laxmann's notes (1769) on an animal found near Barnaul, about 400 km south of Novosibirsk, USSR. The first recognized fossil zokors were described by Milne-Edwards (1874) from material collected near Peking and in Nei Mongol, China. Since Milne-Edwards's time, fossils have been assigned to the group from deposits identified stratigraphically from the Miocene through the Pleistocene in Mongolia and northern China (Nehring, 1883; Schlosser, 1924; Teilhard de Chardin, 1926, 1940, 1942; Boule and Teilhard de Chardin, 1928; Teilhard de Chardin and Young, 1931; Young, 1934; Wood, 1936; Qiu, 1988). The profusion of primitive and derived forms, described from the same horizons and localities in China and Mongolia, poses complex taxonomic problems. As the geology of China and Mongolia is now being charted with rigor, some of the problems may be resolved.

Soviet paleontologists have listed fossil zokors from Pliocene and Pleistocene horizons of western Siberia, Kazakhstan, Transbaikalia, and northern Mongolia (Devjatkin and Zazhigin, 1974; Vangengeim et al., 1975; Adamenko, 1976; Arkhipov, 1977; Sarsekov and Gu'skova, 1979; Zazhigin, 1980; Pokalitov, 1985). Systematic and genetic studies of Recent forms in the USSR have also been published (Ognev, 1947; Kuznetsov, 1965; Martynova, 1975; Vorontsov and Martynova, 1976; Martynova et al., 1977). However, phylogenetic studies of the Soviet fossil material have not reached the west.

This paper describes a new cranium from Shanxi and discusses myospalacine relationships and distribution. It is affectionately dedicated to Karl F. Koopman, friend, mentor, and goad.

METHODS AND MATERIALS

DEFINITIONS: I follow Wahlert (1974, 1985) for names of cranial foramina, Bugge (1971) for cephalic arteries, and Reig (1977) for dental topography. Reig's terms are used as topographic guidelines and without assumptions about homology.

Clinomegodont and *orthomegodont* follow Teilhard de Chardin (1942). As this paper of Teilhard's is not readily available, I repeat his definitions here:

"1. *orthomegodont* pattern (crown not

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Fig. 1. *Myospalax psilurus* skeleton, from Milne-Edwards (1874).

elongated; median labial lobe symmetrical).

"2. *clinomegodont* pattern (crown elongated procumbent forward; median labial lobe asymmetrical).

"Although well marked on the other teeth too, the opposition between orth- and clinomegodont patterns is especially clear on upper M2" (Teilhard de Chardin, 1942: 33).

Occipital shield is defined as the central area of the occipital bone dorsal to the foramen magnum, defined laterally by vertical ridges.

Lateral occipital fossae or *lateral occiputs* are the regions lateral to the occipital shield formed by occipital, mastoid, and squamosal bones.

MEASUREMENTS: Skull measurements for adults of the sample studied are listed in table 2. A skull was considered adult if the basioccipital/basisphenoid junction was united and if the vertical ridges defining the occipital shield were acute and not rounded.

Braincase width was measured at the masseteric notch. Width of the occipital shield was measured at the widest portion of the shield. Height of the occipital shield was measured from the dorsalmost point of the foramen magnum to the dorsalmost point of the occipital shield.

SCOPE: This study includes both fossil and Recent forms of Myospalacinae. Data have been collected from specimens at the institutions listed below and information in the literature has also been used. Not all named forms in the literature have been included in this report. Where a form is known only from an isolated tooth ("*Prosiphneus*" *intermedius*) or rostrum and lower jaws (*P. sinensis*), it has been excluded. Such material does not provide enough characters to support a phylogenetic hypothesis. Forms have been included for which skulls have been referred, such as *P. wongi* (Pei, 1936). The teeth Wood (1936) described as *Prosiphneus lupinus* have not been included, as they have been identified as *Plesiodipus leei,* an early cricetodontine, by Li and Qiu (1980).

SPECIMENS EXAMINED

ABBREVIATIONS: F:AM = American Museum of Natural History, Frick Collection, Department of Vertebrate Paleontology; AMNH = American Museum of Natural History, Department of Mammalogy; USNM = National Museum of Natural History, Mammal Division; BMNH = British Museum of Natural History, Mammal Section.

LOCALITIES: Localities are given as they appear on specimen tags. The gazetteer, following the specimen list, gives the pinyin name, the label name in parentheses, and where possible, coordinates.

FOSSIL

CHINA: Shansi, Pai tao tsun

Myospalax fontanierei: F:AM 125799, 125800, 125802
Myospalax tingi: F:AM 125794–125798
Myospalax chaoyatseni: F:AM 125793
Myospalax sp.: F:AM 125801

RECENT

CHINA:

Myospalax fontanieri Milne-Edwards
- Hopeh: Lao tas tzu: AMNH 56852, 56853
- Shansi: Wu-tsai: AMNH 37857; USNM 172633, 172635, 172636, 172638, 172639
- Chiao cheng shan: USNM 155082
- Ningwu-fu: BMNH 9.1.1.209
- Shensi: Fengsiang fu: AMNH 32297
- Yu-ling: USNM 155083, 155084, 155086–155088; BMNH 9.1.1.216
- Kansu: Ching-ning: USNM 155172–155180
- Lanchow: USNM 240751, 240753–240755
- Choni: USNM 240898

Myospalax rothschildi Thomas
- Kansu: Archuen: AMNH 60420
- Tao chou: BMNH 11.11.1.2 (Type); USNM 144023–144027

Myospalax smithi Thomas
- Kansu: No locality: AMNH 60419
- Lanchow: USNM 240750, 240752
- Choni: USNM 240899
- Tao chou: BMNH 11.11.1.1 (Type), 12.8.5.58
- Szechwan, Jesila: USNM 255141

Myospalax aspalax Pallas
- Mongolia: High Plateau: BMNH 67.12.2.24

Myospalax epsilanus Thomas
- Manchuria: Kirin, Hsiaoling: USNM 270434, 270435
- Khingan Mts.: BMNH 10.5.1.75 (Type), 10.5.1.71–10.5.1.74, 10.5.1.76–10.5.1.80

Myospalax psilurus Milne-Edwards
- Hopei: Yangtsien near Tientsin: BMNH 8.2.23.1, 8.10.4.1

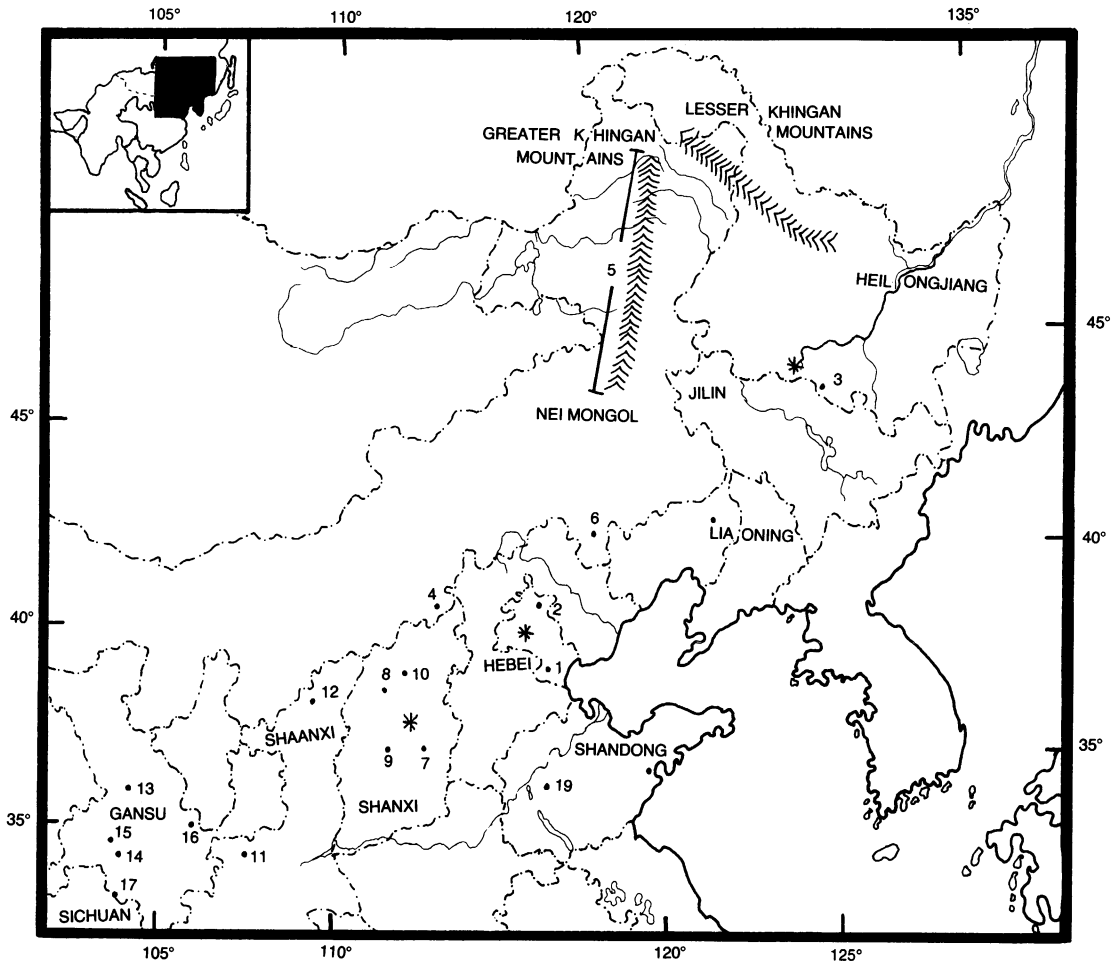

Fig. 2. Distribution of *Myospalax* in China based on specimens examined. **1.** Yangstien. **2.** Lao tas tzu. **3.** Hsiaoling. **4.** Chahar, Eul-che-san-hao. **5.** Greater Khingan Mountains. **6.** Chifeng. **7.** Bai Tao Cun. **8.** Wuzhai. **9.** Jiaocheng. **10.** Ningwu. **11.** Fengxiang. **12.** Yulin. **13.** Lanzhou. **14.** Jone. **15.** Lintan. **16.** Jingning. **17.** Ashuen. **19.** Jinan.

Chihli: Ch'ih-feng: BMNH 14.8.26.7, 14.8.26.8, 16.1.1.9
Shantung: Tsinan: BMNH 26.2.3.14

USSR:

Myospalax myospalax Laxmann
Kazakh SSR: East Kazakhstan, Katon-karagay: AMNH 178801
Semipalatinsk Prov.: AMNH 206573
RSFSR: Gorno-Altayskaya, Dapucha: USNM 175196
Altai Mts.: BMNH 45.4.21.4, 43.12.19.6, 42.4.26.4, 7.1.1.158
Altai, Tocherga: BMNH 9.9.1.8
Altai: BMNH 28.6.19.56, 28.6.19.57
Western Siberia: BMNH 78.12.28.8

GAZETTEER

Chinese localities are shown in figure 2. Localities in the USSR are indicated in figure 3.

The type locality for *Myospalax aspalax* (= *M. armandi*) is usually given as "Mongolia," or "High Mongolian Plateau." Pere David's journal for 1866 is more precise and gives the type locality as the environs of the Mongolian village that David (1867) called Eul-che-san-hao. Pere David's diary entry for April 4, 1866, states that he left China from the village of Sin-pin-keou (orthography David's) and passed through the Great Wall.

"After a short rest at Tien-Dze, we leave on our left the Yang-Ho . . . in order to climb toward the northwest." He arrived at Eul-che-san-hao at 6 in the evening. As David usually covered about 30 miles a day, it can be safely assumed that the type locality of *M. aspalax* is within 30 miles of the Great Wall, approximately 50 miles northeast of Datong and about 31 miles northwest of Yanggao (locality 6 in fig. 2).

In the catalog of his Mongolian collection, Pere David indicated that the animal he had called *Spalax talpinus* had been identified by Milne-Edwards as *Siphneus armandi* (David, 1867: 27). Pere David reached Eul-che-san-hao on April 4, 1866, and remained there until April 18. The following entry appears under the date April 10:

"Grâce à l'humidité, le *Spalax talpinus,* aux longs ongles, a commencé à travailler; on remarques ses taupinières fraiches, deux ou trois fois plus grosses que celles des taupes communes et ordinairement disposées en longue ligne. Ces animaux paraissent être assez nombreux ici: je parviens à m'en procurer un."

and on April 12

"Nous acquérons d'autre echantillons de Spalax, tandi qu'un Lièvre se laisse tuer par le frère pour venir renforcer notre souper" (David, 1867).

CHINA:

Hebei (Hopeh)
  Yangstien near Tianjinn, 39°08′N, 117°12′E
    Lao tas tzu, 100 mi NE Beijing
Jilin (Kirin)
  Hsiaoling, 45°22′N, 127°17′E
Nei Mongol (Chihli)
  Chahar, Eul-che-san-hao (David's orthography)
  Greater Khingan Mountains
  Chihfeng, 42°17′N, 118°53′E
Shanxi (Shansi)
  Bai Tao Cun (Pai tao ts'un), 37°46′N, 112°50′E
  Wuzhai, 38°51′N, 111°48′E
  Jiaocheng (Chiao-ch'eng shan), 37°33′N, 112°09′E
  Ningwu (Ning-wu-fu), 39°01′N, 112°18′E
Shaanxi (Shensi)
  Fengxiang (Fengsiang), 34°31′N, 107°24′E
  Yulin (Yu-ling), 38°18′N, 109°45′E
Gansu (Kansu)
  Lanzhou (Lanchow), 36°03′N, 103°41′E
  Jone (Choni), 34°35′N, 103°32′E
  Lintan (Tao cheo), 34°43′N, 103°40′E
  Jingning (Ching-ning), 35°30′N, 105°45′E
  Ashuen (Archuen of G. M. Allen, 1940: 934), Min Shan Mts. (Lönnberg, 1926: 8)
Sichuan (Szechwan)
  Jesila: unable to locate
Shandong (Shantung)
  Jinan (Tsinan), 36°40′N, 117°E

USSR:
Kazakh SSR
  East Kazakhstan; Katon Karagay, 49°11′N, 85°37′E
  Semipalatinsk: Znamenka, 50°04′N, 79°31′E
RSFSR
  Gorno-Altayskaya, Dapucha (not located)
  Altai Mountains
  Altai, Tocherga (not located)

Acknowledgments

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SYSTEMATICS

MATERIAL: A small cranium, F:AM 125801, with some red sandy matrix adhering and with partial bullae, right incisor and cheek teeth in place (fig. 4).

LOCALITY AND HORIZON: Collected in 1935 by Kan Ch'uan Pao for Childs Frick at Pai tao ts'un (Bai Tao Cun), Shanxi, People's Republic of China (Frick Archives, vol. 132). Pai tao ts'un is approximately 14 miles southwest of the city of Shouyang and approxi-

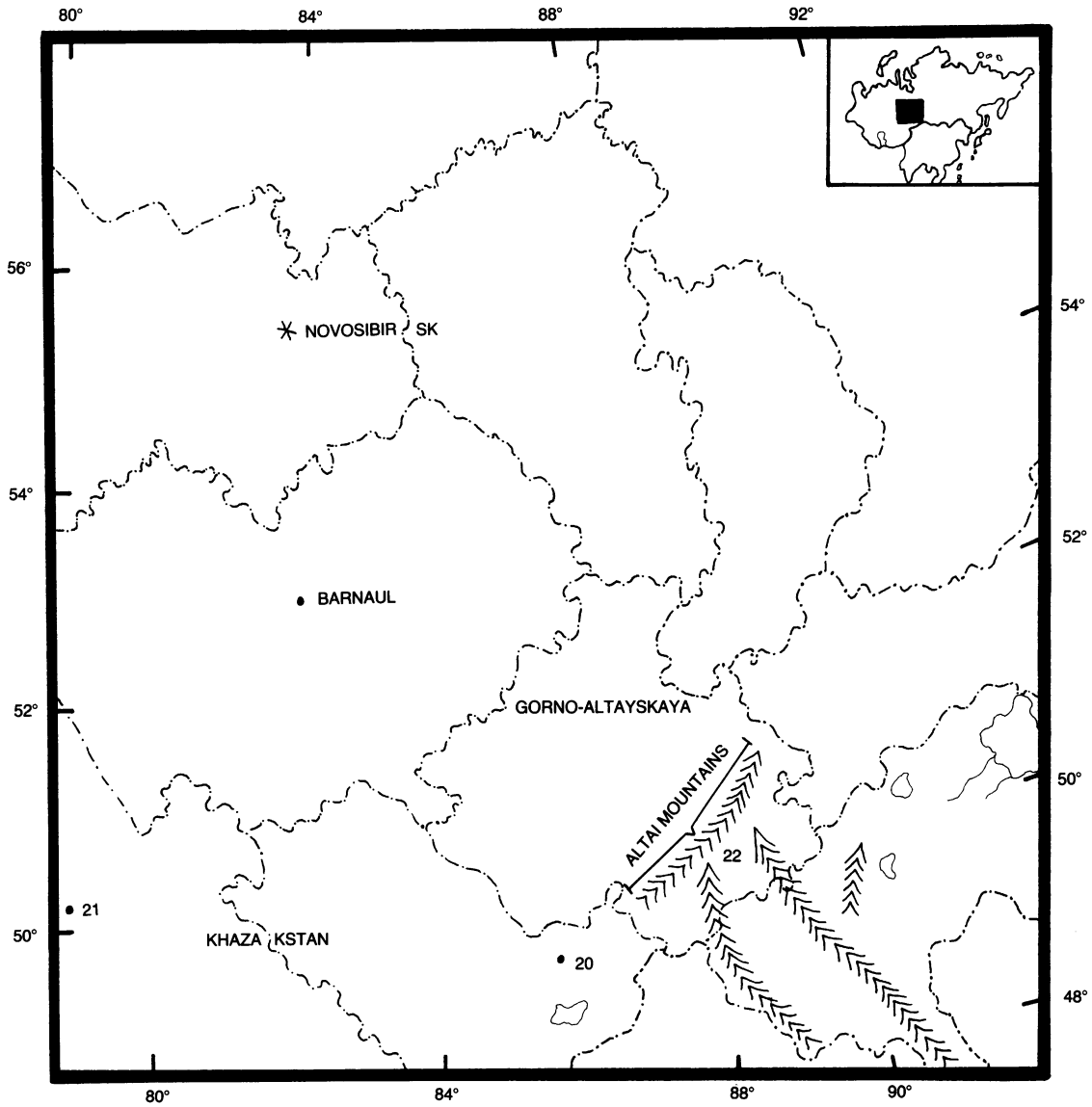


Fig. 3. Distribution of *Myospalax myospalax* in USSR based on specimens examined. **20.** Katon Karagay. **21.** Znamenka. **22.** Altai Mountains.

mately 23 miles east-southeast of the city of Taiyuan. Collection records indicate that the cranium was among a group of fossil rodents that "occur above the main *Hipparion* beds" (Frick Archives, vol. 132, December 17, 1935). Dr. Richard Tedford, Department of Vertebrate Paleontology, has kindly supplied the following stratigraphic note:

> The mammalian fossils from the "Hipparion beds" at Bai Tao Cun are a late Miocene assemblage typical of faunas of the Baodean Mammal Age in China. . . . The *Myospalax* species packaged with the specimen described here include the living *M. fontanieri* and the extinct *M. tingi* and *M. chaoyatseni*, all taxa that occur widely in the upper part of the Wucheng Loess in Shanxi and Shaanxi provinces. Evidence from the Luochuan district in central Shaanxi province (Liu, 1985: 31–36, 67–72), where the rodent biostratigraphy is calibrated paleomagnetically, indicates that this association of *Myospalax* species occurs in the early Matuyama Chron above and below the Olduvai subchron and is thus of latest Pliocene or earliest Pleistocene

age. That this is not an unlikely age for the taxon described here as well is indicated by the occurrence of very similar rooted myospalacines in faunas attributed to the late Pliocene or early Pleistocene (the "Villafranchian" of Teilhard 1940) elsewhere in north China.

DESCRIPTION: The cranium is well preserved and dull white. Brasicranial sutures appear fused, and the other sutures are joined but clear. The occiput is flat, set at right angles to the parietal and squamosal, and lies in the same vertical plane as the lateral occipital fossae. A well-defined lambdoid crest rises parallel to the supraoccipital crest but does not merge with it.

The weak temporal crests bordering the narrow sagittal area merge into the lambdoid crest and converge as they approach the orbits. The nasals widen gradually from the frontal suture to the end of the rostrum and bow slightly near the anterior tips. The tips of the nasals are missing, as are the jugals.

The squamosal root of the zygoma begins halfway between the top and bottom of the braincase and extends posteriorly to the occiput. The maxillary root of the zygoma is broken in a manner that defies determination of the tilt and shape of the zygomatic plate.

Incisive foramina are about 38 percent of the length of the diastema and barely extend into the maxilla. The median suture of the maxillaries forms a ridge that continues along the median suture of the palatine bones and projects from the posterior palate as a median spinous process. The posterior tip of this extension is broken.

Palatine bones form the medial walls and roof of the parapterygoid fossae, which slope posterodorsally. The lateral walls of the fossae are formed by the maxillary tooth capsule from mid-M2 to the posterior edge of M3. There is a gap or pocket medial to and behind M3 where palatine and maxillary bones do not join. Posterior to the gap, the palatines bend dorsally and with a small portion of the maxilla form the anterior wall of the pterygoid fossae. The pterygoid fossae are moderately deep, but do not form pockets dorsal to the basisphenoid. The palatines meet the basisphenoid dorsal to the anterior third of the hamular processes to form the medial walls of the fossae. The alisphenoid forms the dorsal walls of the fossae and joins the palatine and maxilla anterolaterally. An open channel marks the posterior edge of each pterygoid fossa. The channel ends in the posterior alar foramen.

The posterior opening of the masticatory-buccinator nerve canal is laterodorsal to the pterygoid fossae and hidden when the bulla is intact. This canal is 2.4 mm long and has one anterior opening, the combined masticatory-buccinator foramen. A channel passes dorsally to the masseteric notch, and a second channel passes anteroventrally across the lateral surface of the maxilla. I interpret the first as the path of the masseteric nerve and the second as the groove for the buccinator nerve.

As ventral parts of the bullae are missing, the presence or absence of a stapedial foramen cannot be determined. The carotid canal is visible between the intact medial bullar wall and the basioccipital approximately midway between the suture with basisphenoid and occipital condyles.

The occipital area is cracked, but a clearly defined occipital shield and lateral fossae are visible. The bones forming the occipital area can also be seen. The occipital plate does not extend to the outer edges of the lateral fossae at the dorsum. A narrow band of the squamosal extends from the lambdoid ridge ventrally for about three-quarters of the length. The ventral part of the lateral fossae is formed from the mastoid.

The capsule of the maxilla that contains the molar roots contacts the orbitosphenoid bone. Optic and ethmoid foramina are dorsal to this abutment. The ethmoid foramen is in the orbitosphenoid–frontal suture, anterior and dorsal to the optic foramen.

The upper incisors are almost square in cross section and extend into the maxilla almost to the anterior face of M1. The incisor enamel is orange. Occlusal surfaces of the molars are omega-shaped with two prominent buccal flexi. The lophs of M1 cross the long axis of the toothrow obliquely, but those of M2 and M3 are more nearly at right angles to this axis. Lingually the molars lack enamel except around the closed-off hypoflexus. A slight indentation in the edge of the anterior enamel of the anterocone may indicate the presence of a protoflexus in unworn teeth. The buccal walls of each tooth are encased in a thick band of enamel that is interrupted

Fig. 4. *Myospalax youngi,* F:AM 125801. Approximately ×2.

by a dentine tract at or near the salient angles (see fig. 10). Maxillary bone was removed on the right side to determine root development. Each molar has a single closed root. The root of M1 is formed by the fusion of two prongs. The labial dentine tracts extend dorsally onto the roots of the teeth (fig. 5). Buccal flexi extend dorsally to approximately 2 mm from

Fig. 5. *Myospalax youngi,* F:AM 125801. Right side prepared to expose molar roots. ×8.

the base of each root. Other measurements are given in table 1.

COMPARISONS: I compared the cranium with fossils described in the literature, as well as specimens of *M. tingi, M. chaoyatseni,* and *M. fontanieri* in the Frick fossil collection and with living forms of *M. aspalax, M. myospalax, M. psilurus, M. epsilanus, M. fontanieri, M. smithi,* and *M. rothschildi* in the collections of the National Museum of Natural History, the American Museum of Natural History, and the British Museum (Natural History). I include in *M. fontanieri* the taxa *cansus, fontanus,* and *baileyi.*

The extinct *tingi* group of myospalacines—*M. paratingi, M. praetingi, M. omegodon, M. tingi, M. trassaerti, M. chaoyatseni,* and *M. epitingi*—differs from F:AM 125801 by possessing the following characters: concave occiput (fig. 6A), M1 well developed, enamel-clad protoflexus and hypoflexus, and pterygoid fossae that are excavated deeply to extend dorsal to the basisphenoid.

Fossil *M. fontanieri* and the Recent species *M. fontanieri, M. smithi,* and *M. rothschildi* possess characters that distinguish them markedly from F:AM 125801: a pronounced convexity of the occipital shield (fig. 6C), rootless molars, third molar elongate and often with a posteroflexus, pterygoid fossae that extend in pockets dorsal to the basisphenoid, channel in posterior wall of pterygoid fossa rather than at posterior rim, and carotid canal located at suture between basisphenoid and basioccipital.

The Recent species with a flat occiput (fig. 6B)—*M. myospalax, M. psilurus, M. epsilanus,* and *M. aspalax*—differ from F:AM 125801 by their clinomegodont, rootless molars, and molar occlusal patterns. *M. myospalax, M. epsilanus,* and *M. psilurus* have a protoflexus and hypoflexus on M1. Some populations of *M. myospalax* lose the protoflexus with wear. *M. aspalax* differs by its greatly reduced M3.

The new skull differs significantly from the flat-occiput fossil forms: *M. arvicolinus, M. truncatus, M. lyratus, M. pseudarmandi,* and *M. wongi.* The first three are large crania, over 44 mm in length, with rugose crests and ridges as well as distinguishing molar characters. The molars of *M. lyratus* and *M. truncatus* are brachydont with unfused roots. The rootless clinomegodont molars of *M. arvicolinus* have

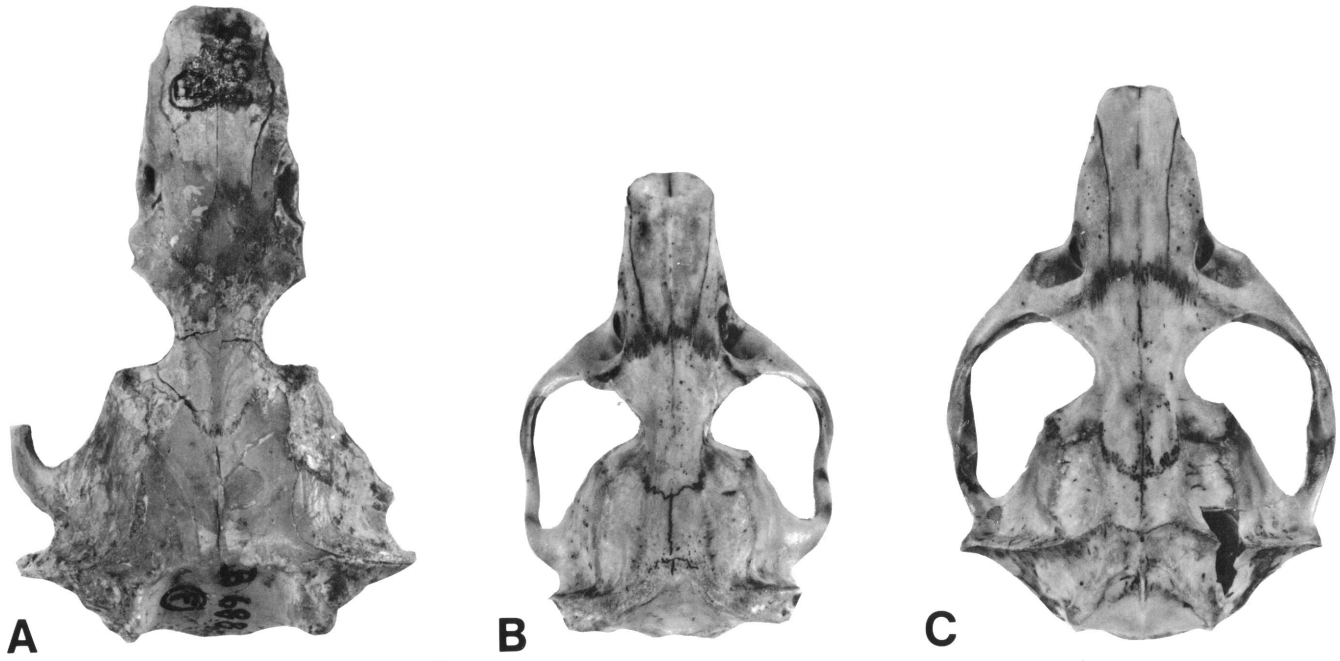


Fig. 6. *Myospalax* dorsal view showing concave, flat, and convex occipital shapes. **A.** *M. tingi* (F:AM 125798). **B.** *M. myospalax* (AMNH 206573). **C.** *M. fontanieri* (AMNH 56852). Approximately ×1.5.

TABLE 1
Cranial Measurements (in millimeters) of Flat-Occiput Fossil *Myospalax* and *M. youngi*

	?youngi	*youngi*[a]	*truncatus*[b]	*lyratus*[b]	*pseudarmandi*[c]
Condylarbasal	38.6	–	46.0	45.0	40.0
Least frontal	6.5	–	6.0	8.0	6.5
Occipital width	23.4	–	25.0	30.0	25.0
Occipital shield width	15.4	–	–	–	–
Occipital shield height	11.9	–	18.0	17.0	20.0
Upper diastema length	10.8	–	14.0	14.5	12.5
Alveolar length M1–M3	8.9	–	9.5	10.0	–
M1–M3 length	8.7	–	9.5	10.0	8.0/8.2[d]
M1–M2 length	6.3	6.5	–	–	–
M1 height	8.1	9.0	6.0	7.0	8.2[e]
m1–m3 length	–	9.0	–	–	9.0
m1 length	–	6.0	–	–	–
Lower diastema length	–	6.0	–	–	6.0[f]

[a] Teilhard de Chardin, 1940: 66.
[b] Teilhard de Chardin, 1942: 49.
[c] Teilhard de Chardin, 1940: 67–77.
[d] Type series skulls 2–6.
[e] Type series skull 4.
[f] Type series jaw 8.

a well-developed protoflexus on M1; otherwise, the lingual faces of the teeth are without flexi and almost straight. The rootless, clinomegodont dentition and further reduction of M3 in *M. pseudarmandi* appear to represent a more derived condition than that seen in F:AM 125801. The upper dentition of *M. wongi* lacks any vestigate of a protoflexus on M1 (Pei, 1936: fig. 40; pl. IV, fig. 20).

Although *M. youngi* is known only from a lower jaw with dentition and a rostrum with M1 and M2, I compared it to the Frick fossil because of similarities in the dental morphology and size. The drawing and photograph of the two upper molars (Teilhard, 1940: pl. II, figs. 4, 5) show *M. youngi* with an indentation on the anterocone of M1 and fused, two-pronged roots of M1 similar to the skull described here. The drawing accompanying the original description depicts the occlusal pattern as orthomegodont. The photograph of the *M. youngi* occlusal pattern is ambiguous (taken at an angle) and shows the tip of M2 paracone (the diagnostic lobe) to be missing. It is difficult to determine from the photograph whether the teeth are clinomegodont or orthomegodont. Teilhard de Chardin, who defined clinomegodonty (1942) and made the original description of *M. youngi* (1940), described its dentition as clinomegodont in his revision of the genus (Teilhard, 1942).

If Teilhard's 1942 evaluation is correct, *M. youngi* is more derived than F:AM 125801. If the drawings with the original description are correct, the M1 and M2 of F:AM 125801 and *M. youngi* are alike in morphology and development. With only a rostrum and partial upper dentition for *M. youngi,* it cannot be determined if the diagnostic characters of placement of carotid canal, morphology of pterygoid fossae and occiput, and length of upper toothrow are similar as well. The problem cannot be resolved until cranium and lower jaws of *M. youngi* are found in association. With the data available, the identity of the two forms cannot be falsified and I therefore provisionally refer F:AM 125801 to *M. youngi* and give a new diagnosis for that taxon.

SUPERFAMILY MUROIDEA MILLER AND GIDLEY, 1918

SUBFAMILY MYOSPALACINAE LILLJEBORG, 1866

FAMILY MURIDAE CARLETON AND MUSSER, 1984

Genus *Myospalax* Laxmann, 1769

Myospalax youngi Teilhard, 1940

DIAGNOSIS: A small myospalacine (see Carleton and Musser, 1984, for diagnostic characters of the subfamily) with the following suite of characters: flat occiput, shield

height 77 percent of width; slight temporal ridges intersecting acute lambdoid ridge; sagittal area narrow, tapering toward orbits; orthomegodont, single-rooted molars decreasing gradually in length from M1 to M3; upper molars with closed off hypoflexus and two deep buccal flexi; glassy dentine layer on lingual side of upper molars, enamel circling hypoflexi only; posterior tip of incisive foramina enclosed by maxillary; bony palate anterior to posterior lobe of M3; moderately excavated pterygoid fossae with channel open posteroventrally on posterior rims; carotid canal posterior to basioccipital-basisphenoid suture, between bulla and basioccipital bone.

CHARACTER ANALYSIS

In order to place *M. youngi* within the Myospalacinae a character analysis of the genus was done. The characters used are mainly those of skull and teeth, constraints determined by the need to include both fossil and Recent material. Where character polarities follow the hypotheses of others, it is indicated. Where I hypothesize polarity, my reasons are given.

1. *Occiput:* **0,** flat—occipital shield at right angles to dorsal surface of skull, in same plane as lateral occipital fossae; **1,** concave—dorsal shield anterior to lateral fossae; **2,** convex—posterior to lateral fossae. A flat occiput is characteristic of the earliest known rodent skulls. Myospalacine concave and convex occiputs are both derived from this condition. Examples of the three states are shown in figure 6.

2. *Supraorbital shape and braincase:* **0,** supraorbital smooth and rounded, braincase smooth; **1,** supraorbital a shelf, either parallel or hourglass-shaped, weak temporal ridges extending to lambdoid ridge; **2,** strong ridge or bead on supraorbital, temporal ridges pronounced. The definition and ranking of this character follows Musser and Newcomb (1983). Among myospalacines temporal ridges become more distinct with age, but only in one Recent species, *M. smithi,* can they be considered pronounced.

3. *Zygomatic plate:* **0,** anterior margin of zygomatic plate does not extend anterior to dorsal root of zygoma; **1,** margin of plate extends to root of incisor and anterior to dorsal root of zygoma; **2,** margin of plate extends anterior to root of incisor (fig. 7). The forward extension of the zygomatic plate is derived from the primitive rodent condition and a muroid character (Carleton and Musser, 1984). States follow Carleton (1980).

4. *Nasals:* **0,** anterior margins project beyond anterior of incisor face; **1,** anterior margins do not project beyond incisor face. The primitive state is found in paramyids and sciuravids. All myospalacines possess the primitive condition.

5. *Alisphenoid canal:* **0,** alisphenoid bone extended anteriorly, canal open medially; **1,** alisphenoid canal an open channel not separated from masseteric–buccinator foramina by bone. Wahlert (1985) considered the anterior extension of the alisphenoid bone with canal ending in anterior alar fissure primitive for Rodentia. Musser and Newcomb (1983), though stating it differently, recognized this as primitive for murids. I have followed Musser and Newcomb for the derived condition. In myospalacines, the alisphenoid canal is primitive (fig. 8).

6. *Tympanic bullae:* **0,** small and unmodified; **1,** moderately inflated in relation to length of skull; **2,** greatly inflated. I have adapted Musser and Newcomb's (1983) polarities for this character. Although Carleton's (1980) bullae ratios may be a more objective method of rating this character, I was unable to reliably repeat the measurements required.

7. *Incisive foramina length:* **0,** short, terminate anterior to molar row; **1,** long, terminate at M1 or posterior to it. Polarity here follows Musser and Newcomb (1983). Wahlert (1985) hypothesized a ratio of incisive foramen length to diastema of 41–46 percent as primitive for rodents. Incisive foramina in myospalacines terminate well anterior to the upper molar row and are 33–50 percent of diastema length.

8. *Incisive foramina—bone penetration:* **0,** posterior tip of foramina penetrate maxillary bone; **1,** foramina entirely within maxillary bone; **2,** foramina bisected by premaxillary–maxillary suture. This character can be misinterpreted and should be determined on fully prepared specimens under the microscope. A narrow flange of premaxillary bone, not visible to the naked eye, often surrounds the

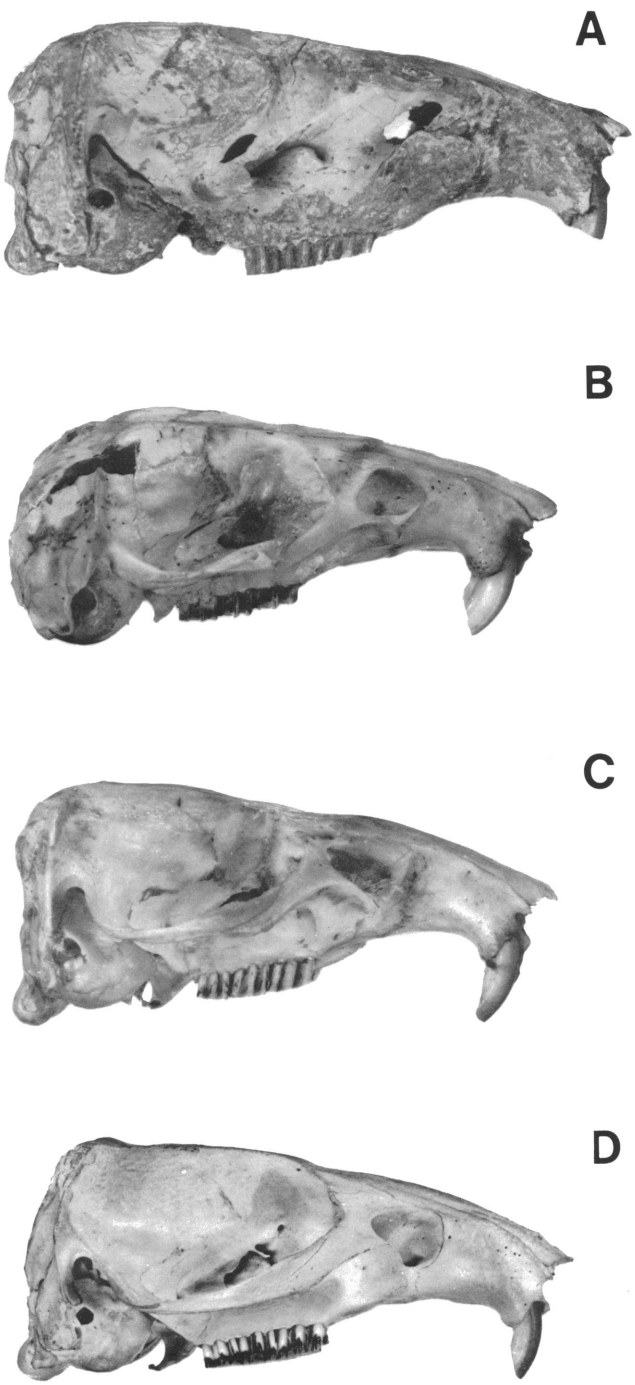


Fig. 7. Right lateral views of *Myospalax* species. **A.** *M. tingi* (F:AM 125798). **B.** *M. fontanieri* (AMNH 56852). **C.** *M. myospalax* (AMNH 206573). **D.** *M. epsilanus* (USNM 270435). Approximately ×1.5.

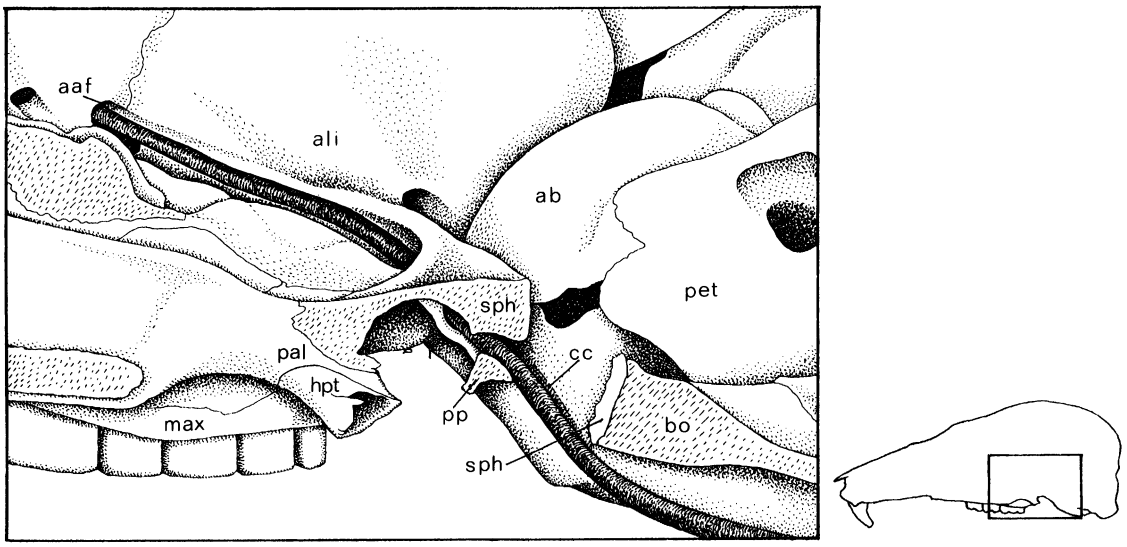


Fig. 8. Sagittal section through pterygoid region of *Myospalax rothschildi* (USNM 144026), diagramming arterial course. aaf, anterior alar fissure; ab, auditory bulla; ali, alisphenoid; bo, basioccipital; cc, carotid canal; hpt, hamular process of pterygoid; max, maxillary; pal, palatal; pet, petrosal; pp, posterior pterygoid rim; sph, basisphenoid.

foramina. Wahlert (1985) considered states 0 and 2 the polarities in rodents. I have arbitrarily included state 1. True polarities for this character will be determined only by analyzing the complex relationships between changes in rostrum length, hypertrophy of nasal organs and nasal innervation, and the morphology of the upper dentition.

9. *Posterior bony palate:* **0,** posterior rim even with or anterior to posterior M3; **1,** posterior rim extends posterior to M3. These are the primitive and derived conditions for murids hypothesized by Musser and Newcomb (1983). The primitive condition is possessed by all myospalacines.

10. *Bony palate surface:* **0,** flat; **1,** slightly grooved; **2,** deeply grooved. The polarities here are an interpretation of part of Hershkovitz's (1962) palatal characters.

11. *Posterolateral palatal pits:* **0,** absent, or one of two small apertures; **1,** multiple pits. The polarities follow Carleton (1980). *Myospalax* combines a slightly grooved palate in adults with a variable number of small posterolateral pits.

12. *Palatine foramina:* **0,** round pair at maxillary–palatine junction; **1,** oblong pair extending into both bones; **2,** large pair with many tiny collateral perforations. Wahlert (1974) considered 0 the primitive rodent condition. The derived conditions follow Carleton (1980).

13. *Parapterygoid fossae:* **0,** absent; **1,** present. These are the posterior palatine fossae of some authors. The palatal bones lateral and posterior to the palatal bridge are sculptured to form fossae that are posterodorsal to the palatine bridge and anteroventral to the pterygoid fossae. As these fossae are present only in highly derived groups, such as arvicolines and myospalacines, I hypothesize their absence as primitive.

14. *Mesopterygoid fossae:* **0,** fossa as wide as palatal bridge; **1,** fossa ⅓ to ½ width of palatal bridge. In the older literature this structure is called the choanae. Polarities follow Musser and Newcomb (1983).

15. *Sphenopalatine vacuities:* **0,** absence of vacuities; **1,** narrow slits or short apertures; **2,** large, wide vacuities. Wahlert (1985) recognized complete absence of vacuities as primitive in rodents. Carleton (1980) found the three character states among Neotomine–Peromyscine rodents. In all of the myospalacines examined, these vacuities are long slits or long narrow apertures.

16. *Pterygoid fossae:* **0,** flat or shallow; **1,** moderately excavated, pockets not dorsal to basisphenoid; **2,** deeply excavated, pockets extend dorsal to basisphenoid. Musser and Newcomb (1983) are followed for polarities, but degrees of derivation have been added. In myospalacines, the lateral walls of these fossae are formed by the maxillary and alisphenoid bones and in some cases a part of the palatine. This is unlike the arvicoline condition, where only the alisphenoid bone forms the lateral fossae walls. Hinton (1926) showed that with age these fossae deepen in arvicolines. Although many of the USNM specimens were very young, I did not find age correlated with depth of fossae in myospalacines.

17. *Foramen ovale:* **0,** present; **1,** absent. The foramen ovale is present throughout the living Muridae, and Wahlert (1974, 1985) recorded it in the early fossil paramyids and sciuravids. I hypothesize that its absence is a derived condition in rodents.

18. *Stapedial foramen:* **0,** present; **1,** absent. I follow Wahlert (1985) in considering the absence of the stapedial foramen as the derived condition.

19. *Sphenofrontal foramen:* **0,** present; **1,** absent. The absence of this foramen is the derived condition (Carleton, 1980; Walhert, 1985). The derived conditions of both sphenofrontal and stapedial foramina "reflect complex changes in the carotid circulation to the orbit and the brain" (Carleton, 1980: 41).

20. *Posterior rim of pterygoid platform:* **0,** simple platform of alisphenoid bone; **1,** open channel along platform rim, oriented posteroventrally; **2,** channel placed as in 1, but partly bone covered; **3,** channel slightly anterior to posterior rim; enclosed by alisphenoid bone; **4,** posterior rim of platform a bone bar, open channel dorsal to bar, in posterior wall of pterygoid fossa. This character, like 18 and 19, indicates changes in the carotid circulation from the primitive condition. I hypothesize degrees of derivation of this character for myospalacines in correlation with other derived characters of the skull and teeth (fig. 9).

21. *Carotid canal:* **0,** between tympanic bulla and midlength of basioccipital bone; **1,** at suture of the basioccipital and the basisphenoid. Wahlert (1985) was vague about polarities for this character. My hypothesis of polarity may be falsified when the functional significance of major variance in cranial circulation is better understood.

22. *Postglenoid vacuity:* **0,** small or absent; **1,** present. In the primitive rodent condition, this is a small foramen that pierces the squamosal ventral to the zygoma and posteromedial to the glenoid fossa (Wahlert, 1974). The muroid condition, derived from the primitive rodent state, is an embayment in the posterior part of the squamosal dorsal to the periotic (Wahlert, 1985). Myospalacines possess the muroid condition.

23. *Masticator-buccinator foramina:* **0,** separate; **1,** joined; **2,** united with foramen ovale accessorius. As these foramina are clearly separate in the paramyids and sciuravids, I hypothesize that a derived condition exists when they are joined in one aperture and that this condition is less derived than their union with the foramen ovale accessorius. Myospalacines vary within state 1 for this character. Some animals have a single aperture on one side, and on the opposite side of the cranium two foramina within the aperture.

24. *Sphenopalatine foramen:* **0,** bound by frontal, maxillary and palatine bones; **1,** hidden by tooth capsule or absent. This foramen was not located in any myospalacine, fossil or Recent, that I examined. If present, it was hidden by bony capsule of maxillary enclosing the molar roots. The foramen may be visible in forms with lower crowned, rooted teeth. At present I consider state 1 a synapomorphy for the genus.

25. *Ethmoid foramen:* **0,** in frontal–orbitosphenoid suture; **1,** surrounded by frontal. All myospalacines examined possess the primitive rodent condition hypothesized by Walhert (1974).

26. *Optic foramen:* **0,** surrounded by orbito-sphenoid; **1,** confluent with sphenoid fissure. The polarities for ethmoid and optic foramina are those of Wahlert (1974).

27. *Components of lateral occiput:* **0,** occipital and mastoid bones; **1,** squamosal, mastoid, and occipital bone. In the primitive condition, the posterior braincase is formed by occipital and mastoid bones. Involvement of the squamosal bone in formation of the lateral occiput is derived. In myospalacines,

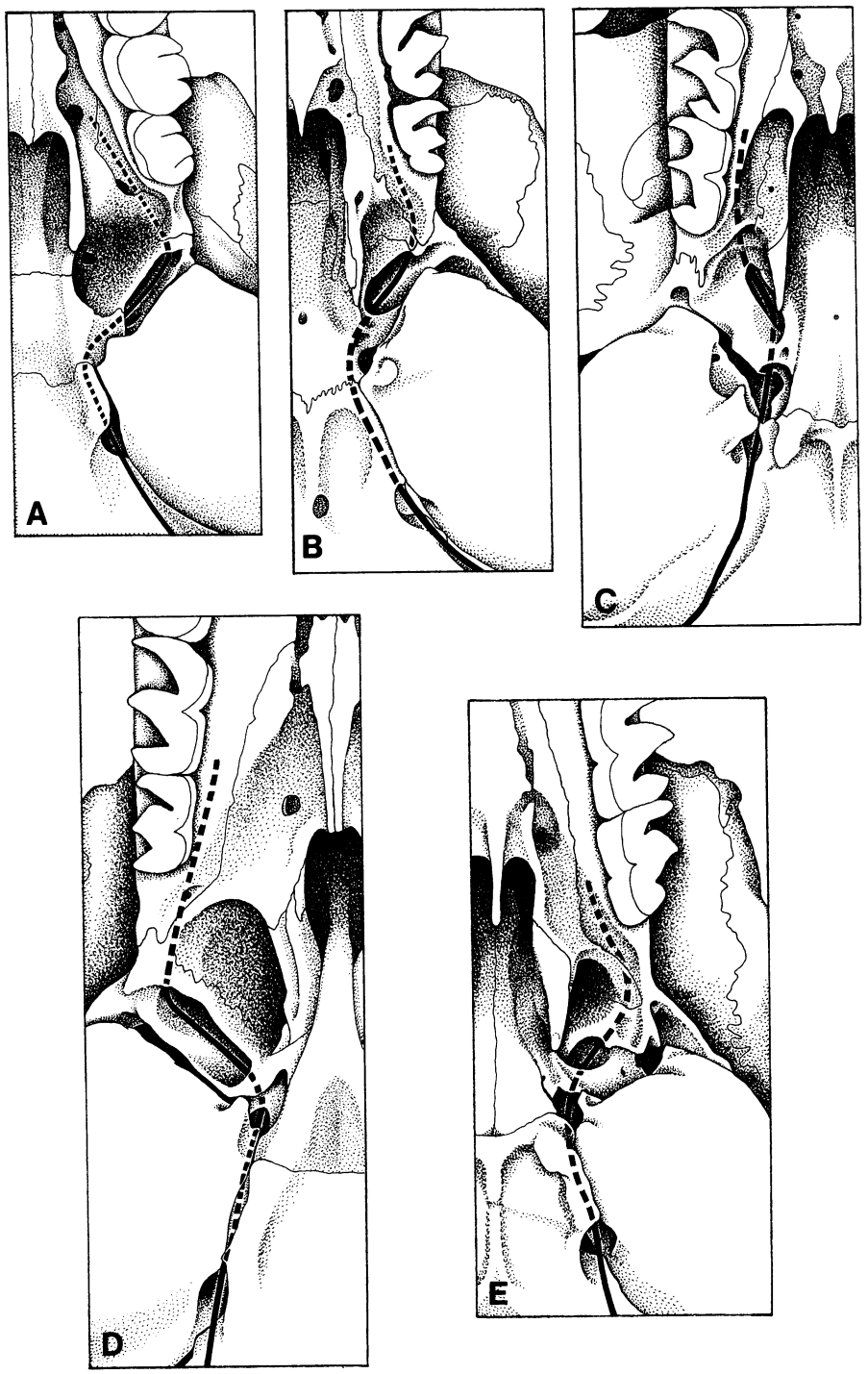


Fig. 9. Posterior pterygoid region of *Myospalax* species. Arterial paths diagrammed. **A.** *M. youngi* (F:AM 125801). **B.** *M. myospalax* (AMNH 206573). **C.** *M. fontanieri* (AMNH 56852). **D.** *M. tingi* (F: AM 125797). **E.** *M. epsilanus* (immature) (USNM 270435).

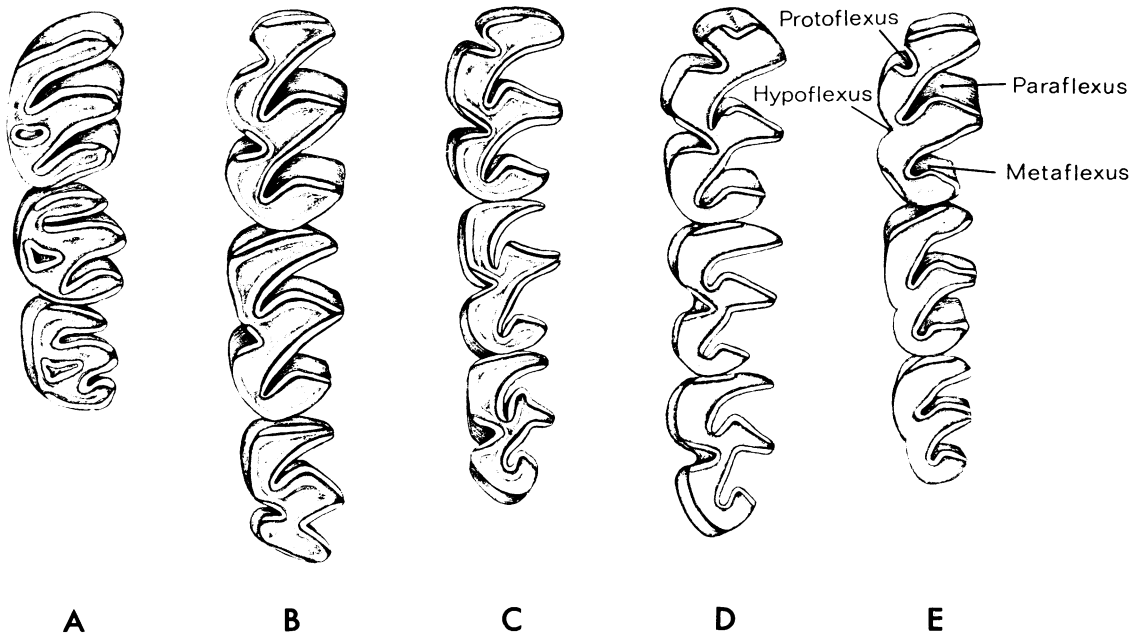


Fig. 10. Distribution of molar enamel in species of *Myospalax*. **A.** *M. youngi* (F:AM 125801). **B.** *M. tingi* (F:AM 125797). **C.** *M. epsilanus* (USNM 270435). **D.** *M. fontanieri* (AMNH 58652). **E.** *M. myospalax* (AMNH 206573).

the squamosal forms about one-fourth of the latral occiput. The mastoid is not inflated.

28. *Color of upper incisor enamel:* **0,** yellow to deep orange; **1,** cream or white.

29. *Incisor tips:* **0,** unnotched; **1,** notched. For character states 29 and 30, Musser and Newcomb's (1983) polarities for primitive murids are followed. For both characters, myospalacines are primitive.

30. *Grooves on incisors:* **0,** ungrooved; **1,** grooved. Carleton's (1980) polarities are followed for this character. Myospalacine incisors are not grooved.

31. *Molar enamel:* **0,** intact for circumference of tooth crown; **1,** interrupted by dentine tracts at salient angles of anterocone, paracone, and metacone; **2,** on upper lingual and lower buccal, enamel present only around paraflexus(id) and hypoflexus(id). There is a layer of glassy dentine medial to the enamel around the circumference of myospalacine molar crowns (fig. 10). It can be seen with the microscope on clean specimens and is unmistakable in ultraviolet light. The glassy dentine has been interpreted as enamel because the teeth are usually illustrated as if the enamel circumferences of the crown were intact. Ellerman (1941: vol. 2, 544) depicted accurately the enamel distribution on BMNH 28.6.19.56, *Myospalax myospalax,* which is incorrectly identified as *M. psilurus.* It should be noted that there is considerable variation in extent of enamel cover of anterior face of the anterocone(id) of the first molars and the posterior face of the third molars. Anteromedian flexus on M1 (fig. 10D) is occasionally found in *Myospalax fontanieri.* Polarities are based on the hypothesis that distribution of enamel only around hypoflexus(id) and paraflexus(id) is the result of expansion of dentine tracts on anterolingual conule, anterolabial conulid, protocone(id), and hypocone(id). States 1 and 2 are present in the fused rooted F:AM 125801. Polarities will not be precisely determined until fossil myospalacine bunodont, rooted molars are studied for this character. Von Koenigswald (1980) examined the molar enamel structure in one fossil and one Recent myospalacine (both species unknown). He found the enam-

el structure in both to be primitive radial enamel. Radial enamel may be another myospalacine synapomorphy.

32. *Molar topography:* **0,** bunodont rooted molars; **1,** planar, molars relatively high crowned with cusps flattened and even in height; **2,** hypsodont, rooted; **3,** hypsodont, evergrowing. For this character, I used Carleton (1980) for polarities.

33. *Upper molar roots:* **0,** molars with three roots; **1,** molars with two roots; **2,** molars with one root; **3,** rootless. This progression has been documented in the Muridae, in South American cricetines, and in arvicolines. The three derived conditions have been reported in fossil myospalacines. All Recent members of the genus are rootless.

34. *Relative molar length:* **0,** decrease gradually in length from first molar to third; **1,** third molar much reduced, less than 60 percent length of first; **2,** third molar subequal to or longer than first. I hypothesize these polarities for myospalacines from measurements in the literature and from the specimens I studied. Conditions 1 and 2 are both derived from 0.

35. *Cusp positions of second molar:* **0,** paracone opposite hypoflexus; **1,** paracone anterior to hypoflexus. The primitive condition corresponds to Teilhard's orthomegodont condition, in which the tooth crown is not elongated and the paracone lobe is symmetrical. The derived condition corresponds to Teilhard's definition of clinomegodont, in which the crown is elongated and the paracone lobe asymmetrical and procumbent forward.

36. *Lingual flexi on first upper molar:* **0,** with well-developed protoflexus and hypoflexus; **1,** protoflexus disappears with moderate wear, hypoflexus persists; **2,** with hypoflexus only.

37. *Lingual flexi of third upper molar:* **0,** with protoflexus and hypoflexus; **1,** with hypoflexus only; **2,** without flexi.

38. *Buccal flexi of upper molars:* **0,** all with paraflexus and metaflexus; **1,** third molar with metaflexus only; **2,** third molar with para-, meta-, and posteroflexus. Characters 37 through 39 might be grouped together but have been kept separate for clarity. Characters are stated in terms of flexi rather than cusps, as I have serious doubts about cusp homology. The dentition of these rodents is highly derived (fig. 11). It is not clear whether the external lobes derive from a cusp and the nearest loph, from either structure alone, or from a medial cusp and external style. The least derived upper occlusal pattern seems to be a first molar with protoflexus and hypoflexus but second and third upper molars with hypoflexus only. In all upper molars, the paraflexus and metaflexus form the embayments of the "omega" pattern. The posteroflexus is shown in figure 11C. This character is variable in the species *fontanieri, smithi,* and *rothschildi.*

39. *Lingual flexids of lower molars:* **0,** first and second molars with deep meta-, mesa-, and entoflexids, third molar with mesaflexid and entoflexid; **1,** first molar with weak metaflexid and strong mesa- and entoflexids, second and third molars with mesaflexid and entoflexid only; **2,** all molars with strong metaflexid and entoflexid.

40. *Buccal flexids of lower molars:* **0,** protoflexid and hypoflexid on each molar; **1,** first molar with protoflexid and hypoflexid, second with hypoflexid only, third without flexid; **2,** first molar as in 1, second and third with shallow hypoflexid; **3,** first and second molars with protoflexid and hypoflexid, third molar without flexid. In the least derived forms the lower molar embayment pattern is formed by the protoflexid and hypoflexid. As in the upper dentition, the cusp homology of the posterior lobe is in doubt. A case can be made for derivation from either a biserial or triserial condition.

41. *Plane of angular process of dentary:* **0,** in same plane as ascending ramus; **1,** lateral to ramus approximately 45 degrees. Both Carleton (1980) and Repenning (1968) rated the laterally deflected angular process as derived. The myospalacine angular process is derived.

42. *Arvicoline groove on dentary:* **0,** groove absent; **1,** groove present. The arvicoline groove is a sharp, narrow groove posteroventral and parallel to the anterior edge of the ascending ramus. It meets the lower masseteric crest ventral to m1 and marks the insertion of the anterior part of the middle masseter muscle (Repenning, 1968). Repenning hypothesized that presence of the groove was derived from a primitive cricetine condition.

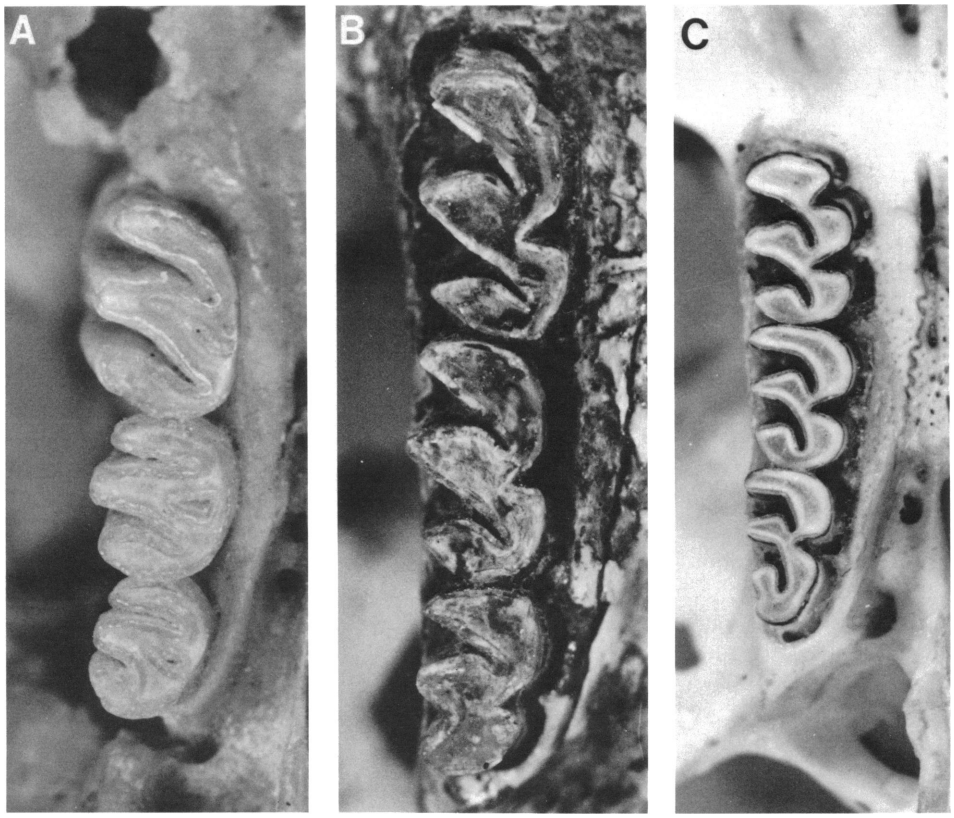


Fig. 11. Zokor right molar rows. **A.** *M. youngi* (F:AM 125801). **B.** *M. tingi* (F:AM 125798). **C.** *M. rothschildi* (AMNH 20420). **D.** *M. epsilanus* (USNM 270435). **E.** *M. myospalax* (AMNH 206573). **F.** *M. fontanieri* (AMNH 56852). ×10.

I suggest that absence of the groove is the primitive murid condition.

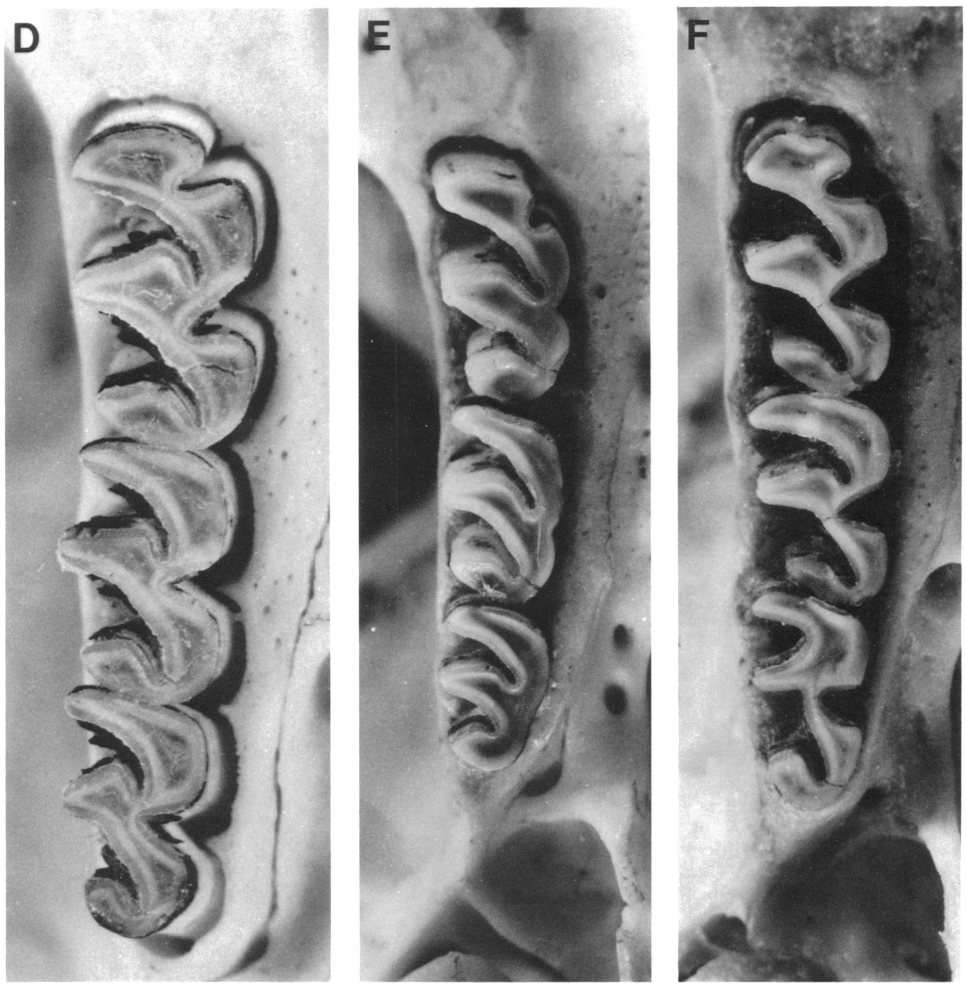
43. *Hallux:* **0,** hind foot first digit with claw; **1,** hind foot first digit with very short claw; **2,** hind foot first digit with nail. Polarities are those of Musser and Newcomb (1983). All Recent myospalacines have the derived murid very short claw. The condition in fossils was not determined.

44. *Mastoid foramen:* **0,** a slit between dorsal mastoid and occipital bones; **1,** small formen between dorsal mastoid and occipital; **2,** absent. Wahlert (1985) is followed for this character; however, I have split Wahlert's derived character and consider the absence of this foramen as most derived.

RESULTS

The results of the character analysis are presented in the following discussion of characters and the cladogram. Arabic numbers in the following text correspond to those in the cladogram (fig. 12). Information about the pterygoid region or cranial foramina for many of the named fossils is not available from the literature. Only those seen or for which there is information about character states are included. The hypothesis presented is that myospalacines, fossil and Recent, are a closely related group of species derived from a primitive muroid stock.

1. Primitive muroids: (a) occiput flat—at right angles to dorsal braincase; (b) supraorbital region smooth or with low lateral ridges; (c) anterior margin of zygomatic plate extends to root of incisor and anterior to dorsal maxillary root of zygoma; (d) nasals extend anterior to face of incisors; (e) alisphenoid canal open to cranial cavity on medial side of alisphenoid bone; (f) moderately in-



flated bulla; (g) incisive foramina anterior to M1, not elongated; (h) incisive foramina within premaxillary or only posterior tip in maxillary bone; (i) posterior edge of bony palate anterior to posterior margins of M3; (j) round pair of palatine foramina at maxillary-palatine junction; (k) sphenopalatine vacuities slits or narrow; (l) pterygoid fossa shallow and completely roofed; (m) carotid canal between bulla and midlength of basioccipital bone; (n) postglenoid vacuity present; (o) ethmoid foramen in frontal orbito-sphenoid suture; (p) optic foramen surrounded by orbito-sphenoid bone; (q) mastoid foramen a slit; (r) arvicoline groove absent from dentary; (s) incisor enamel orange to deep yellow; (t) tips of incisors not notched; (u) incisors ungrooved; (v) hallux with claw instead of nail.

2. Synapomorphic myospalacine characters: (a) bony palate slightly grooved; (b) multiple pits on bony palate; (c) parapterygoid fossa present; (d) mesopterygoid fossa ½ to ⅓ width of palatal bridge; (e) foramen ovale and foramen ovale accessorius absent; (f) squamosomastoid foramen absent; (g) stapedial foramen absent or minuscule; (h) sphenofrontal foramen absent; (i) open channel along posterior rim of both pterygoid fossae; (j) masticator-buccinator foramina in one aperture; (k) sphenopalatine foramen hidden by tooth capsule; (l) squamosal, mastoid, and occipital bones form lateral occiput; (m) mo-

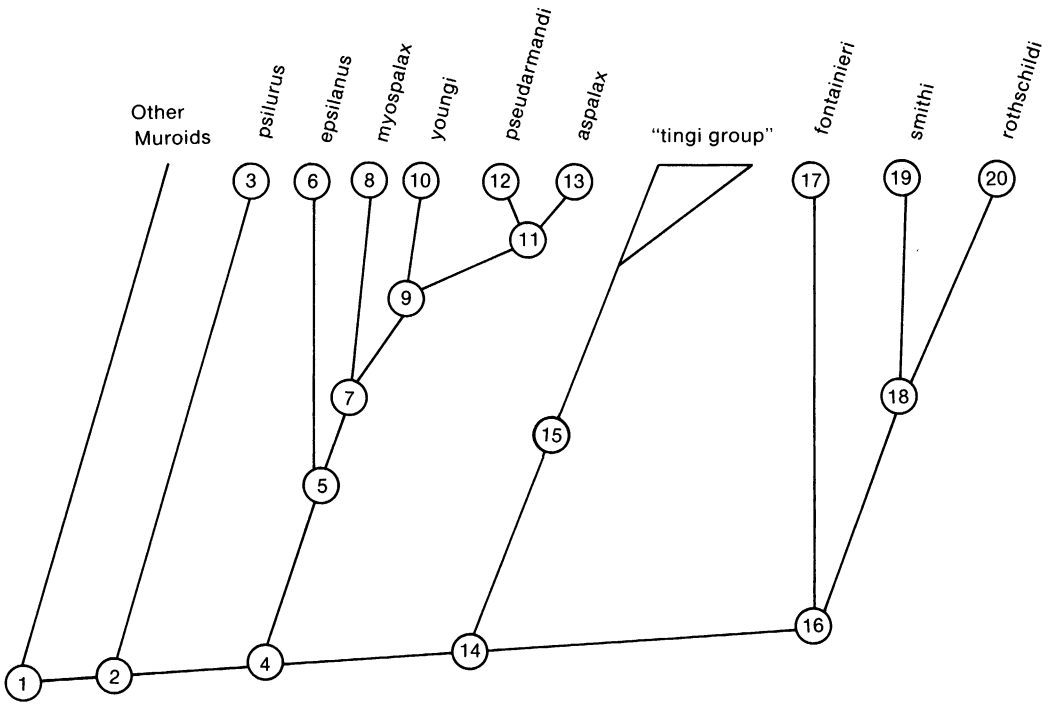


Fig. 12. Proposed myospalacine relationships. Numbers at nodes correspond to numbers in text.

lar enamel absent from salient angles of anterocone(id), paracone, metacone(id), entoconid; present only around protoflexus(id) and hypoflexus(id); (n) omegodont molars relatively high crowned with cusps flattened to a planar surface; (o) gradual decrease in length from first to third molar; (p) paracone opposite hypoflexus of second molar; (q) first upper molar with well-developed protoflexus and hypoflexus; (r) third upper molar with hypoflexus only; (s) all upper molars with paraflexus and metaflexus; (t) first lower molar with weak metaflexid but strong mesoflexid and entoflexid; (u) all lower molars with protoflexid and hypoflexid; (v) angular process of dentary laterally deflected about 45 degrees.

3. *Myospalax psilurus.* Molars clinomegodont, hypsodont, and rootless.

4. Pterygoid fossa moderately deep, does not extend dorsal to basisphenoid.

5. Length of M3 less than 80 percent that of M1.

6. *M. epsilanus.* Molars clinomegodont, hypsodont, and rootless. In adults, internal maxillary artery passes through bone of pterygoid fossa. It can be traced by a ridge from basisphenoid to the alisphenoid canal. In immature specimens, posterior rim of fossa does not reach the bulla and the channel is partly open (fig. 9E).

7. Pattern of molar flexi simplified.

8. *M. myospalax.* Molars clinomegodont, hypsodont, and rootless. Second and third lower molars lose protoflexid with slight wear. Some adult specimens have no enamel on buccal side of second and third lower molars.

9. Upper molar flexi simplified.

10. *M. youngi.* Orthomegodont molars with two roots that are fused. Third upper molar 63 percent of M1. First upper molar may have protoflexus that disappears with wear, leaving a barely discernible dent in enamel. Second and third molars with hypoflexi that close off in wear, leaving enamel fossettes.

11. Third upper molar reduced further. Occlusal pattern clinomegodont.

12. *M. pseudarmandi.* Molars rootless; dentine tracts almost reach base of tooth.

13. *M. aspalax.* Third upper molar less than 50 percent of M1. Molars hypsodont,

rootless, with dentine tracts to base of tooth. Channel at posterior rim of pterygoid fossa open for half its length in BMNH 67.12.1.14 (only specimen seen).

14. Deep pterygoid fossa extending dorsal to basiphenoid. Incisive foramina bisected by maxillary–premaxillary suture.

15. Concave occiput. Myospalacines sharing this character are the extinct forms that Teilhard called the *tingi* group. He demonstrated the evolution from relatively low-crowned double rooted molars to complete rootless hypsodonty in this group (Teilhard de Chardin, 1942).

16. Convex occiput. Carotid canal at basioccipital–basisphenoid suture. Posterior rim of pterygoid fossa a bony ridge. Open internal maxillary channel in posterior wall of pterygoid fossa dorsal to bony ridge.

17. *M. fontanieri.* Large size: condylobasal length 39.3–46.6 mm. M3 85–95 percent of M1. Posteroflexus variably present on M3.

18. Smaller size. M3 with lingual protoflexus and hypoflexus. Buccal posteroflexus always present on M3.

19. *M. smithi.* Condylobasal range 35.4–41.2 mm. M3 85–100 percent of M1. Bulla notably more flattened than rest of genus. Temporal ridges pronounced in adult.

20. *M. rothschildi.* Condylobasal range 31.4–33.7 mm.

I consider myospalacines, fossil and Recent, to be one genus. Placing species that have not achieved complete rootless hypsodonty in the separate genus *Prosiphneus* is an artificial division of a monophyletic group. Four species groups are identified. Subgeneric names are not assigned. *Myospalax psilurus* is alone in the first group. Except for rootless hypsodonty, it retains the most primitive characters of the genus.

Members of the second species group—including *M. epsilanus, M. myospalax, M. aspalax,* and the fossils *M. youngi* and *M. pseudarmandi*—have deepened the pterygoid fossa and the more derived members of the group have simplified the dental occlusal pattern. I separate *M. aspalax* from *M. myospalax* because of the extreme reduction of M3 and the loss of flexi in the upper molars in *M. aspalax.* The karyological and biochemical data (Martynova, 1975; Martynova et al., 1977) also support recognizing *M. aspalax* as a separate species.

The fossils *M. omegodon, M. praetingi, M. paratingi, M. chaoyatseni, M. trassaerti, M. tingi,* and *M. epitingi* form the third, or *tingi,* group. Apparently they have no living members and they share the characters of concave occipital shield, pterygoid fossa extending dorsal to the basisphenoid, and incisive foramina bisected by the premaxillary–maxillary suture.

The fossil and Recent *M. fontanieri* and the Recent species *M. smithi* and *M. rothschildi* are the members of the most derived group. They share the characters of convex occipital shield, carotid canal at the basioccipital-basisphenoid suture, a bony ridge as the posterior rim of the pterygoid fossa, and the channel in the posterior wall of the deep pterygoid fossa. The earliest known fossils in this group are completely hypsodont and rootless (Teilhard, 1942). They occur in the same assemblages as less derived and rooted forms of the other species groups.

I place incertae sedis, until further study: *M. licenti, M. murinus, M. wongi, M. arvicolinus, M. truncatus,* and *M. lyratus.* Also incertae sedis are the named forms known only from maxillary or mandibular fragments or isolated teeth: *M. eriksoni, M. sinensis,* and *M. intermedius.*

Of the 44 characters studied, myospalacines possess 22 characters of primitive rodents (1, 5, 8, 12, 21, 25, 42, 43, 44) or primitive muroids (2, 3, 4, 6, 7, 9, 15, 22, 23, 26, 28, 29, 30). The 22 derived characters are associated with hypsodonty (10, 11, 13, 14, 16, 24, 32, 33, 41), dental occlusion modifications (31, 34, 35, 36, 37, 38, 39, 40), cranial circulation changes (17, 18, 19, 20), and skull reinforcement (27).

The equal division of characters between plesiomorphic murid features and derived characters associated with fossorial adaptation lends support to the proposal that myospalacines are derived from a primitive murid stock that made an early adaptation to a fossorial habit.

The character complex myospalacines share with arvicolines is a set of parallel adaptations for propalinal chewing of tough, fibrous plant material. These include excavated pterygoid fossa, laterally deflected angular pro-

TABLE 2

Cranial Measurements (in millimeters) of Adult Recent *Myospalax*[a]

	M. aspalax[b]	*M. psilurus*	*M. epsilanus*	*M. myospalax*	*M. fontanieri*	*M. smithi*	*M. roth-schildi*[c]
Greatest length	42.4	42.4 ± 0.8 (5) 41.5–43.5	44.9 ± 2.2 (11) 41.4–49.3	44.1 ± 2.0 (7) 41.6–46.8	44.7 ± 2.7 (20) 40.2–49.9	43.3 ± 1.9 (6) 40.6–46.2	38.9
Condylarbasal length	39.2	39.1 ± 1.0 (5) 38.5–40.9	41.8 ± 2.6 (11) 37.2–45.3	40.8 ± 1.6 (6) 38.2–43.1	40.1 ± 3.1 (20) 35.7–46.6	37.8 ± 2.1 (6) 35.4–41.2	33.7
Incisive foramina	4.8	4.9 ± 0.5 (5) 4.5–5.7	5.1 ± 0.3 (11) 4.7–5.6	4.8 ± 0.3 (7) 4.3–5.3	6.8 ± 0.6 (22) 5.7–8.3	6.1 ± 0.6 (7) 5.3–7.0	6.0
Bony palate length	21.4	22.5 ± 0.7 (5) 22.1–23.8	24.1 ± 1.3 (11) 21.4–25.8	22.0 ± 1.0 (7) 21.2–23.8	23.1 ± 1.8 (22) 20.2–26.5	20.8 ± 1.0 (7) 19.5–22.1	18.5
Diastema length	14.0	14.2 ± 0.5 (5) 13.6–14.9	15.4 ± 1.0 (11) 13.5–17.1	14.1 ± 0.5 (7) 13.5–14.6	14.6 ± 1.4 (22) 12.2–17.0	13.8 ± 1.0 (7) 13.0–15.3	12.9
Length M1–M3	9.1	10.1 ± 0.6 (5) 9.7–10.9	9.9 ± 0.6 (11) 9.0–11.0	9.5 ± 0.6 (7) 8.9–10.8	10.6 ± 0.7 (22) 9.3–11.8	9.5 ± 0.6 (7) 8.8–10.4	7.6
Least frontal breadth	8.2	7.5 ± 0.4 (5) 6.8–7.8	7.2 ± 0.3 (11) 6.8–7.9	7.5 ± 0.8 (7) 6.5–8.9	7.3 ± 1.2 (20) 6.2–10.2	7.9 ± 0.7 (7) 7.1–9.3	7.7
Braincase breadth at masseteric notch	18.0	17.6 ± 0.7 (5) 16.9–18.4	18.8 ± 0.6 (11) 17.9–19.9	18.3 ± 0.7 (7) 17.5–19.3	18.6 ± 1.5 (20) 16.2–21.3	17.8 ± 0.5 (6) 17.2–18.5	15.9
Height of occipital shield	—	13.3 ± 0.8 (5) 12.6–14.6	13.0 ± 1.4 (11) 10.5–15.2	13.0 ± 0.7 (5) 12.3–14.2	10.9 ± 2.1 (20) 7.3–15.1	9.8 ± 1.0 (6) 8.2–10.8	8.6
Breadth of occipital shield	19.4	16.8 ± 0.7 (5) 16.1–17.8	17.7 ±1.2 (11) 16.1–20.2	19.5 ±1.6 (7) 17.7–22.6	13.6 ± 1.3 (21) 11.5–16.2	13.9 ± 0.9 (6) 12.8–15.1	13.2
Length of M1	4.2	4.0 ± 0.2 (5) 3.8–4.4	3.8 ± 0.2 (11) 3.5–4.2	3.8 ± 0.4 (7) 3.6–4.6	4.0 ± 0.4 (22) 3.3–4.6	3.4 ± 0.2 (7) 3.2–3.8	2.7
Breadth of M3	2.0	2.7 ± 1.0 (5) 2.7–2.8	2.8 ± 0.2 (11) 2.5–3.0	2.5 ± 0.3 (7) 2.2–3.0	3.4 ± 0.4 (22) 2.7–4.0	3.0 ± 0.3 (7) 2.6–3.5	2.5

[a] Mean ± SD, number of specimens (in parentheses), and observed range are listed for *M. psilurus, M. epsilanus, M. myospalax, M. fontanieri,* and *M. smithi.*

[b] BMNH 67.12.2.24.

[c] Type, BMNH 11.11.1.1.

cess, and strong flexi on planar occluding molars. The arvicoline cephalic arterial system, arvicoline dentary groove, foramina ovale and ovale accessorius, bulla construction, and tympanic hook suggest that arvicolines are not close to myospalacines phylogenetically.

FURTHER RESEARCH PROBLEMS

Differences in the shape of the occipital shield have been used to distinguish species of *Myospalax* since Milne-Edwards's day, but no study has been made of the differing occipital muscle attachments in the genus. It is still not known what functional differences the convex and concave occiputs represent. Are these functional differences related to the extinction of the concave-occiput myospalacines?

Anatomical study of the genus has been uneven. Milne-Edwards (1874) described and illustrated the anatomy of the forelimbs, intestines, and caecum. It is not certain which of the species available to him were included in the report or illustrated. Gambarian (1960) compared the myology of *Myospalax myospalax* with that of other burrowing animals, and Vorontsov (1979) reported on the alimentary system of *Myospalax myospalax.* Interspecific studies and comparisons of the muscle and soft tissue systems have yet to be done.

The functional morphology of the posterior rims of the pterygoid fossae needs further study. The fossorial arvicoline *Prometheomys* has a similar structure and no stapedial foramen, but *Ellobius,* the other fossorial arvicoline, lacks the character and has a stapedial foramen.

Carotid cranial circulation in *Myospalax* needs to be studied. Bugge (1970, 1971) did not report on the cephalic arterial systems of either myospalacines or the arvicoline genera *Ellobius* and *Prometheomys.* The posterior pterygoid channel that leads into the posterior alar foramen, and the absence of a stapedial foramen suggest the hypothesis that infraorbital and masseteric blood supply are carried from the internal carotid artery by an anastomosis through the alisphenoid canal similar to those illustrated by Bugge (1971, fig. 3) as a5′ or a4. This hypothesis can be tested and the precise pattern of cephalic arterial supply determined.

Study of molar enamel structure in this genus should add to phylogenetic information. Von Koenigswald (1980) did not have species identifications for the myospalacines he studied. Moreover, his sample was very small (one fossil and one Recent dentition). Determining whether radial enamel is a synapomorphy for the entire genus has still to be done.

An interesting zoogeographic problem is presented by the discontinuous distribution of living myospalacines. *Myospalax myospalax,* collected in the Ob basin and in the Soviet Altai Mountains, is isolated from the rest of the genus, which is known from southeastern Transbaikalia, the greater Kinghan Mountains, Soviet Maritime Province, and the northern Chinese provinces of Nei Mongol, Jilin, Hebei, Shanxi, Shaanxi, and southeastern Gansu. The apparent disjunct distribution may be an artifact of no collections made in northernmost Gansu and the A-erh-t'ai shan (Mongolian and Chinese Altay). It is probable that *Myospalax myospalax* was isolated by the increasing desertification of northwestern China and Mongolia during the Pliocene (Wang, 1984; Zhao and Xing, 1984).

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Postcranial Remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and Other Late Quaternary Mammals from Long Mile Cave, Jamaica

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ABSTRACT

Long Mile Cave (northwestern Jamaica) is the type locality of the extinct late Quaternary primate *Xenothrix mcgregori*. The holotype and only specimen currently referred to this species is an incomplete mandible collected by H. E. Anthony in 1920 and described by E. E. Williams and K. F. Koopman in 1952. Anthony also collected a large number of mammalian postcranial elements at Long Mile; these have never been adequately described. In this paper, we show that an os coxae, femur, and two tibiae from the Long Mile collection are sufficiently primatelike to warrant their allocation to the hypodigm of *X. mcgregori*. Like the holotype jaw, these elements are notably different from their counterparts in living platyrrhines. *Xenothrix* was probably a heavy, slow-moving quadruped or climber, as morphologically distinct from Callitrichidae, Cebidae, and Atelidae as members of these platyrrhine families are from one another. In recognition of this, the family name Xenotrichidae is revived for the reception of *Xenothrix*. Several other postcranials in the Long Mile collection cannot be assigned to *Xenothrix* or to Primates. At least one and possibly two species are represented, but ordinal assignment is precluded by the condition of the specimens. Nevertheless, these finds and others made in the last several years conclusively establish that Jamaica had a more extensive land mammal fauna than heretofore supposed. It is not out of the question that some of the now-extinct taxa (three of which were primates) survived up to early European times, but there is no decisive evidence for this in early written records.

INTRODUCTION

Evidence is accumulating that parts of the West Indies were a significant center of primate evolution and diversification. At least three of the Greater Antilles—Jamaica, Hispaniola, and Cuba—had one or more endemic species of primates that survived into the latter part of the Quaternary (Ford, 1990). Beyond this little else is clear, in part because of a severe lack of good fossil material. Cave deposits are virtually the only context in which remains of extinct Quaternary vertebrates have been discovered in the West Indies, and, unsurprisingly, primate fossils are extremely rare in such depositional settings (MacPhee and Woods, 1982).

Perhaps the most controversial of the extinct primates of the West Indies is the Jamaican species *Xenothrix mcgregori* (Williams and Koopman, 1952; Rosenberger, 1977; MacPhee, 1984; Ford and Morgan, 1986, in prep.; Ford, 1990). Although generally accepted as a member of Platyrrhini, its narrower affinities within the infraorder have remained problematic. The holotype mandible from Long Mile Cave (fig. 1) was recognized as primatelike at the time of its recovery by its discoverer, Harold E. Anthony, although he did not attempt to specify a taxonomic assignment. Williams and Koopman (1952), who ultimately described

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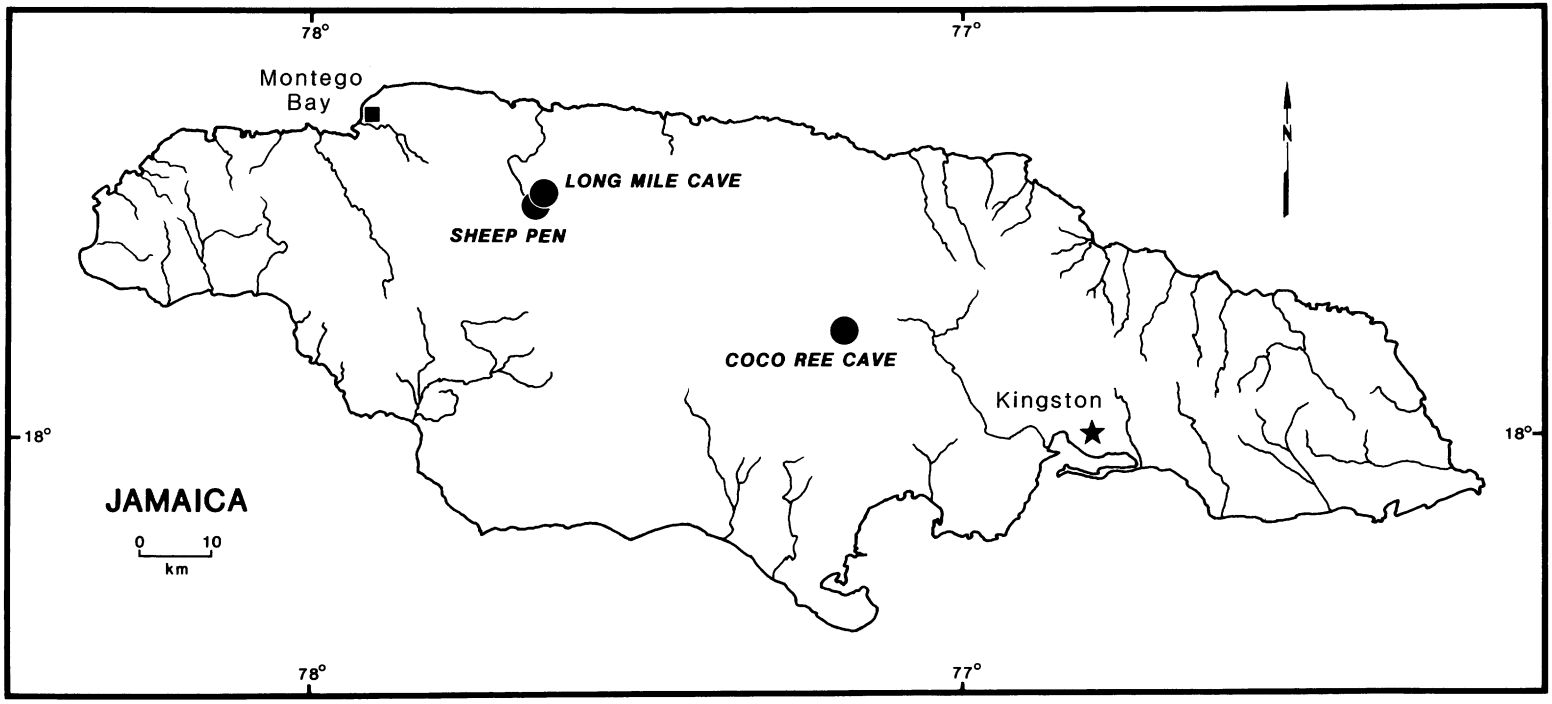

Fig. 1. Sketch map of Jamaica, showing position of localities yielding remains of recently extinct primates.

and named *Xenothrix,* felt unable to conclude anything very specific about its affinities. Noting that *Xenothrix* combined "the dental formula of a marmoset, the expanded [gonial] angle of *Callicebus,* and a dental pattern approximating that of *Cebus*" (Williams and Koopman, 1952: 11), these authors decided that it could be safely referred to an uncertain position within Cebidae. However, since they included all New World monkeys in this family, their stated allocation is not different from Platyrrhini incertae sedis. Hershkovitz (1970) also emphasized the distinctiveness of the Long Mile jaw and remarked on the detailed convergences which its molars display with cheek teeth of the lemur *Daubentonia.* To reflect the morphological isolation of *Xenothrix* among New World monkeys, he created for its reception a new monotypic family, Xenotrichidae (Hershkovitz [1974], emendation of Xenothricidae [Hershkovitz, 1970]).

Rosenberger (1977, 1981) has rejected Hershkovitz' arguments for separate family status and has concentrated on trying to establish the identity of the closest relatives of *Xenothrix.* His original preference was to leave *Xenothrix* in an old-style concept of Cebidae, possibly within a nested "monophyletic group including *Aotus, Callicebus,* and the prehensile-tailed monkeys" (Rosenberger, 1977: 477). In a later cladistic classification of Platyrrhini (Rosenberger, 1981), this early conclusion was considerably modified: *Xenothrix* was identified as the sister taxon of *Callicebus* in the tribe Pitheciini (Pitheciinae, Atelidae), while *Aotus* was placed in the same subfamily, but in a different tribe. The most recent evaluation by Rosenberger and coworkers (Rosenberger et al., 1990) provides additional interpretations favoring the argument that *Xenothrix* shares derived traits with pitheciines.

Until 1984, the holotype jaw (AMNH 148198) of *Xenothrix* was the only primate specimen known from Jamaica. In that year, Ford and Morgan (1984) announced the discovery of a damaged proximal femur (UF 40097), evidently primate, in a faunal collection from Coco Ree Cave in east central Jamaica (figs. 1, 2). On the basis of morphological analyses presented in their detailed description of this find (Ford and Morgan, 1986: 127), they argued that the femur came from a taxon "more closely related to callitrichids than to other platyrrhine clades." Since they provisionally accepted Rosenberger's (1981) view that *Xenothrix* was related to *Callicebus,* they were forced to conclude that UF 40097 represented a second and therefore different lineage of Jamaican monkeys related to marmosets. More recently, the same authors have reported the existence of another primate femur from Jamaica, this time from Sheep Pen rock shelter, situated approximately 2.5 km south of Long Mile Cave (Ford and Morgan, 1988; figs. 1, 2). In their view, this specimen (UF 58350) represents still another platyrrhine species that is neither *Callicebus*-like nor callitrichid-like. If they are correct in their assessments, Jamaica supported at least three species of primates within the very recent past.

The mandible of *Xenothrix* was not the only interesting fossil in the extensive faunal collection that Anthony brought back from Long Mile. In their brief census of other mammalian remains from this locality, Williams and Koopman (1952: 13) reported the existence of several unusual postcranial elements that they were unable to identify to taxon. These specimens have never been described or analyzed systematically, despite their potential relevance for understanding the faunal composition of Jamaica during the Quaternary. In view of the quickening interest in West Indian vertebrate paleontology (Williams, 1989; MacPhee and Wyss, 1990), this is an opportune time to review the significance of this important but neglected material.

Abbreviations

Institutional

AMNH	Department of Mammalogy, American Museum of Natural History
UF	Florida Museum of Natural History, Gainesville

Anatomical

ac	anterior crest (tibia)
am	acetabular margin
ap	process on posterior aspect of femur (for adductores mm.)

Fig. 2. Femora from Jamaican cave sites attributed to Platyrrhini by Ford and Morgan (1986, 1988): **TOP.** UF 58350, from Sheep Pen. **BOTTOM.** UF 40097, from Coco Ree Cave (both specimens to same scale). From left to right, specimens shown in anterior, posterior, lateral, and medial view. Note difference in degree of projection of lesser trochanters in these specimens (large white arrows in posterior views).

as	auricular surface
bg	bicipital groove (intertubercular sulcus)
br	brachialis m. (insertion)
cp	coronoid process
df	dorsal epitrochlear fossa
dpe	deltopectoral eminence
ef	entepicondylar foramen
ff	facet for fabella
ftp	tibialis posterior m. (origin)
gp	gluteal planum
gtb	greater tuberosity
gtr	greater trochanter
ib	interosseous border (ulna)
igs	insertion of gluteus superficialis m.
im	ischial margin
ip	iliac planum
is	infraspinatus m. (insertion)
iss	ischial spine
lc	lateral condyle (femur or tibia)
lsr	lateral supracondylar ridge (humerus)
ltb	lesser tuberosity
ltr	lesser trochanter
mb	"mound of bone" (?for insertion of ischiofemoral ligament on neck of femur)
mc	medial condyle (femur or tibia)
me	medial epicondyle (humerus)
of	olecranon fossa
op	olecranon process
pm	pubic margin
ps	patellar surface
rn	radial notch
sa	ala of sacrum
sap	superior articular process
sl	supracondylar line (femur)
sp	sacral planum
ss	subscapularis m. (insertion)
tm	teres major m. (insertion)
tr	trochlea
tt	tibial tuberosity

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MAMMALIAN POSTCRANIALS FROM LONG MILE CAVE

Long Mile Cave is simply an overhanging rock face, a minor surface feature produced at some uncertain time in the past by the collapse of a gallery roof or cave mouth (for details, see MacPhee, 1984). Over time, loose fill and breakdown have accumulated in the lee of the rock face. This is the deposit from which Anthony recovered his fossil material; the original gallery floor is buried under tons of rock. The age of fossils from Long Mile has not been securely established (MacPhee, 1984), although it is probable that they are late Holocene. Difficulties in dating the time of extinction of *Xenothrix* and other Quaternary mammals of Jamaica are discussed by MacPhee et al. (1989).

Because Anthony never reported on the Long Mile bone sample in print, the only direct source of information about his collecting activities is his field notebook (Anthony, MS), which is preserved in the archives of the Department of Mammalogy of the AMNH. According to his notebook, Anthony worked at Long Mile for a few days in January 1920, excavating bone from the subsurface to a depth of about 1.5 m. Most of the material recovered was described as "coney" (i.e., the endemic capromyid *Geocapromys brownii,* the only living nonvolant native mammal of Jamaica other than the rice rat *Oryzomys couesi antillarum,* whose current status is uncertain). His only specific reference to unusual bones occurs in the entry for January 17, in which he mentioned that his "most important find" for the day was "the lower jaw and a femur of a small monkey, found in the yellow limestone detritus."

In their review of the mammalian material

TABLE 1
Postcranial Remains from Long Mile Cave, Jamaica

Size class	AMNH no.	Element	Condition	Attribution
Large	259900	Right femur	Complete except for damage to ends and trochanters	*Xenothrix mcgregori*
	259904	Left os coxae	Body of ilium, ischial blade partly preserved; symphyseal area lacking	*Xenothrix mcgregori*
	259902	Right tibia	Proximal end, small part of shaft	*Xenothrix mcgregori*
	259903	Left tibia	Proximal end, large part of shaft	*Xenothrix mcgregori*
	259901	Right humerus	Proximal end, small part of shaft	Unattributed
Small	259906	Left humerus	Shaft only	Unattributed
	259905	Right humerus	Partial distal end and shaft	Unattributed
	259907	Left ulna	Proximal end, small part of shaft	Unattributed
	259908	Sacrum	S1 and S2 only	Unattributed

from Long Mile, Williams and Koopman (1952: 13) reported that "[the] femur that Anthony described as associated with the Jamaican jaw has not been found. No such femur was placed with the jaw when the collection came into our hands. However, . . . we found a few limb bones that are not *Geocapromys,* the omnipresent rodent of the cave, and for reasons of erosion and fracture [these] are difficult to identify. These include a femur, two tibiae, and a pelvis."

Of the four bones described as "not *Geocapromys*" by these authors, the os coxae seemed to them the most primatelike. However, Williams and Koopman (1952: 13) refrained from allocating any of this material to *Xenothrix* because of "the lack of any evidence of association beyond presence in the same cave." These finds were given the same catalog number as the holotype mandible of *Xenothrix* (AMNH 148198) in order to facilitate their retrieval from the uncatalogued portion of the Anthony collection.

In the course of our resurvey of the Long Mile collection, we were able to identify five additional elements that also comply with the descriptor "not *Geocapromys*" (table 1). These elements definitely represent at least two different mammals, and they may be grouped in two size classes, a "large" and a "small." The large size class includes the four elements singled out by Williams and Koopman (1952), now individually catalogued. To this group we now add a proximal right humerus (AMNH 259901). Bones in the small size class, previously uncatalogued, include incomplete right and left humeri (AMNH 259905 and 259906), the proximal portion of a left ulna (AMNH 259907), and part of a sacrum (AMNH 259908). The small humeri are obviously from the same species and perhaps from the same individual. Although the ulna cannot be directly articulated with the incomplete left humerus, the relative proportions of these bones are similar. The undistinctive sacral fragment is provisionally included with the small limb bones.

In addition to the foregoing, we found a few other long bone fragments that could not be confidently identified as to element or fitted to any portion of the capromyid skeleton. Some of these may well belong with the elements given extended treatment in the rest of this paper, but in view of their negligible morphological and taxonomic value they will not be discussed further here.

Bones from Long Mile Cave have a reddish brown to pinkish white coloration, probably due to the uptake of pigments from the cave's sedimentary fill. Most of the more complete bones in the Anthony collection are coated with a viscous brown shellac, some of which we were able to remove prior to immersing them in a stronger, acetone-soluble cement. All of the elements to be described here are heavily damaged, in some cases because of poor preparation. The complete fracturing of several of the long bones could have occurred during or immediately after excavation; under high magnification, broken surfaces ex-

hibit step-fractures—usually a sign that a bone was broken in a dry rather than a green condition (Morlan, 1984). The etiology of the numerous, small, randomly oriented pits seen on many Long Mile bones is not known. In our view they do not resemble marks produced by blood vessels (cf. Rosenberger, 1977), teeth, claws, digestive juices, or rolling. Perhaps they were produced by invertebrate scavengers, although we cannot suggest any likely candidates. We cannot exclude the possibility that many of them were created during preparation.

Specimens in the Long Mile sample were compared to a wide variety of Neotropical mammals, including all major groups having past or present representatives in the West Indies (i.e., ceboid monkeys; megalonychid sloths; solenodontid and nesophontid insectivores; and echimyid, capromyid, heptaxodontid, and muroid rodents). This exercise turned up some unexpected character matches whose significance will probably remain uncertain until better material is recovered (e.g., resemblances between the Long Mile femur and that of the arboreal procyonid *Potos flavus*). Proposed attributions, summarized in table 1, are defended in the following sections. Note that none of the specimens in the small size class could be attributed; some of them, at least, seem to be neither rodent nor primate, and we suggest that it can no longer be assumed that these were the only groups that managed to colonize Jamaica.

DESCRIPTION OF POSTCRANIAL ELEMENTS

Specimens are described by size class in the order presented in table 1, which in turn roughly reflects degree of preservation and assignability. Family names and contents for Platyrrhini follow Ford's (1986a) classification.

FEMUR

The Long Mile femur (AMNH 259900) is substantially complete except for its proximal articular end (fig. 3; table 2). We estimate that the maximum length of the bone was approximately 10 cm prior to breakage (table 3, footnote *c*). This specimen exhibits features that tend to distinguish primate femora from those of most other mammals. However, in other respects it differs sharply from the femora of all known platyrrhines (including the Coco Ree and Sheep Pen specimens), and even shows some remarkable resemblances to the femur of the kinkajou *Potos flavus* (fig. 4A–C). Its trait combination is peculiar and therefore requires close analysis.

The most primatelike feature of AMNH 259900 is the apparent size and conformation of the greater and lesser trochanters. Although both processes are broken in this specimen, it is obvious from their stumps that they were large and flared, as in many platyrrhines, strepsirhines, and parapithecids (Fleagle and Kay, 1987). By contrast, in *Potos* and all other Neogene carnivorans examined by us, the lesser trochanter tends to be relatively small and unflared. Other nonprimate Neotropical mammals vary widely in trochanteric morphology, but none is like AMNH 259900 in any important respect. The Coco Ree femur (fig. 2, bottom) also possesses large trochanters, although it differs conspicously from the Long Mile specimen in other ways. The Sheep Pen femur (fig. 2, top) has a smaller lesser trochanter than does any extant platyrrhine examined by us, although Ford (1990) argues that it is within the range of variation for New World monkeys.

A small portion of the root of the femoral neck is preserved (fig. 3D), but there is no indication of the "mound of bone" which Ford (1988) described as present on the posterior femoral necks of all platyrrhines except *Cebus* (?for insertion of ischiofemoral ligament; fig. 2, top). The trochanteric fossa is elongated and deep, somewhat as in the Coco Ree and Sheep Pen specimens, but there is no definable intertrochanteric line or crest. One can feel rather than see an insignificant eminence on the lateral border beneath the root of the greater trochanter. This probably represents the insertion for gluteus superficialis, but it scarcely warrants identification as a third trochanter. A small insertion for gluteus superficialis, general among platyrrhines (Ford, 1980; Ford and Morgan, 1986), is also found in *Potos*. By contrast, the superficialis insertion is prominent in Antillean rodents, sloths, and insectivores.

While the proximal part of AMNH 259900

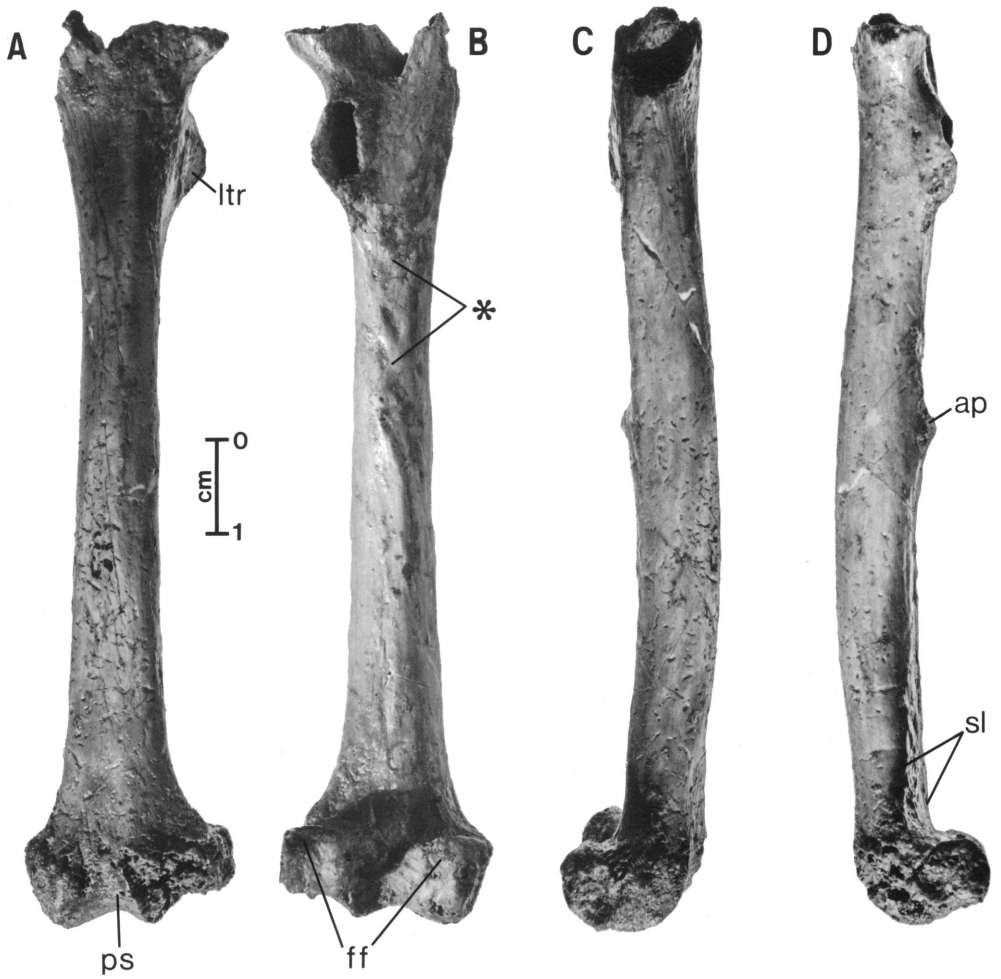


Fig. 3. Femur (AMNH 259900) attributed to *Xenothrix mcgregori,* Anthony collection, Long Mile Cave. Specimen shown in anterior (**A**), posterior (**B**), lateral (**C**), and medial (**D**) view. In posterior view, asterisk indicates complex of strongly defined ridges for insertion of adductores, vasti, and other limb muscles.

does not depart too greatly from typical platyrrhine patterns, its shaft is noticeably different in morphology and proportions. The diaphysis is short, anteriorly convex, and exceptionally robust (figs. 3, 4A, C). Femoral shafts of extant platyrrhines are relatively straight except among callitrichids, in which a slight curvature is seen, and are narrow in proportion to their length—especially among middle-sized and large species. This last point can be easily appreciated by noting that extant platyrrhines with mean midshaft diameters near that of the Jamaican fossil (e.g., *Cebus, Lagothrix*) possess femora whose average lengths are ~25–60% greater (measurements 1 and 3; table 3). Ratio A (table 3), which compares femoral diameter to length, exhibits a narrow range of values because all of the species in the sample have absolutely long femoral lengths compared to widths. All extant nonhominoid primates in the sample fall within the range 0.05–0.07, but AMNH 259900, *Pongo, Potos,* and *Bradypus* exhibit values of 0.09 or greater. (Interestingly, slow-moving *Perodicticus* [0.07] does not place within this group, although for a strepsirhine it has a very robust femur.) Although the Coco Ree and Sheep Pen fem-

TABLE 2

Dimensions (in millimeters) and Indices of Long Mile Postcranials[a]

A. AMNH	259900 (femur)[b]	
	Length, as preserved	*96.2*
	Length, estimated	(~99.0)
	Midshaft, anteroposterior width	9.3
	Midshaft, circumference	29.5
	Intercondylar fossa, width	6.2
B. AMNH	259904 (os coxae)[b]	
	Acetabulum, depth	8.5
	Incisura, width	5.9
	Ventral acetabular margin, breadth	6.3
	Dorsal acetabular margin, breadth	10.3
	Medial acetabular margin, breadth	24.2
	Ischium, length	30.7
	Lower ilium, length	32.1
	Ratio, acetabulum depth/diameter	0.60
	Ratio, acetabulum incisura/diameter	0.42
	Ratio, acetabulum ventral breadth/dorsal breadth	0.61
	Ratio, acetabulum diameter/dorsal + medial + ventral breadth	0.35
	Ratio, lower iliac length/ischium length	1.05
C. AMNH	259903 (tibia)	
	Length, as preserved	*73.3*
	Shaft, mediolateral width (near distal end)	7.0
	Shaft, anteroposterior width (near distal end)	7.5
	Proximal articular surface, mediolateral width, as preserved	*19.5*
	Proximal articular surface, mediolateral width, estimated	(~21.0)
	Proximal articular surface, anteroposterior depth, as preserved	*13.2*
	Proximal articular surface, anteroposterior depth, estimated	(~13.5)
D. AMNH	259902 (tibia)	
	Length, as preserved	*44.3*
	Upper shaft, mediolateral width (near broken end)	7.5
	Upper shaft, anteroposterior width (includes anterior crest)	10.0
	Proximal articular surface, mediolateral width, as preserved	*20.0*
	Proximal articular surface, mediolateral width, estimated	(~21.0)
E. AMNH	259906 (humerus)	
	Length, as preserved	*63.2*
	Lower shaft, anteroposterior width (minimum)	4.9
	Upper shaft, anteroposterior width (deltopectoral)	8.3
	Midshaft, circumference (minimum)	19.9
	Upper shaft, circumference (deltopectoral)	23.5
F. AMNH	259905 (humerus)	
	Length, as preserved	*57.6*
	Lower shaft, anteroposterior width (minimum)	5.0
	Upper shaft, anteroposterior width (deltopectoral)	8.3
	Midshaft, circumference (minimum)	20.0
	Upper shaft, circumference (deltopectoral)	23.8
	Trochlea, proximodistal height	4.4
G. AMNH	259901 (humerus)	
	Length, as preserved	*32.7*
	Upper shaft, mediolateral width	7.8
	Upper shaft, anteroposterior width	9.5
	Upper shaft, circumference	28.1
	Bituberosity width, maximum	14.5
	Intertubercular groove, width	1.8
	Intertubercular groove, depth	1.1
	Head, width	12.7
	Head, length	14.4
	Ratio, width/length	0.88

TABLE 2—(*Continued*)

H. AMNH	259907 (ulna)	
	Length, as preserved	*36.3*
	Height, trochlear notch	9.7
	Upper shaft, mediolateral width (near broken end)	4.3
	Upper shaft, anteroposterior width (near broken end)	5.2
I. AMNH	259908 (sacrum)	
	Length, as preserved (tip of left ala to base of S2)	*27.4*
	Biauricular width at level of S1	24.8
	Sacral canal, anteroposterior width	2.6

[a] Measurements as defined by Fleagle and Simons (1979) or as described in text. "As preserved" measurements are underestimates and are printed in italics.

[b] Additional measurements of femur and pelvis from Long Mile Cave are presented in table 3.

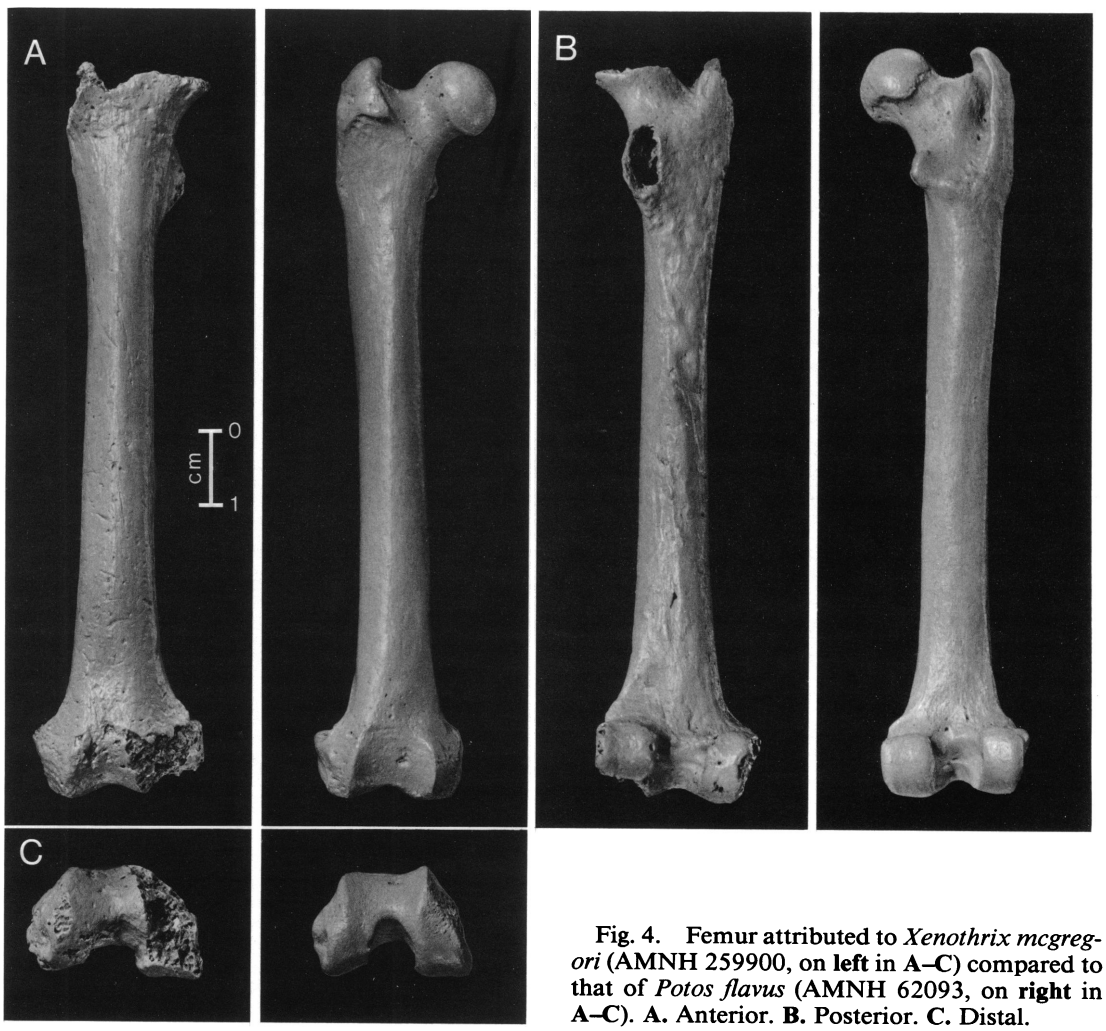


Fig. 4. Femur attributed to *Xenothrix mcgregori* (AMNH 259900, on **left** in **A–C**) compared to that of *Potos flavus* (AMNH 62093, on **right** in **A–C**). **A.** Anterior. **B.** Posterior. **C.** Distal.

ora are incomplete (fig. 2), it is obvious that their shafts are not nearly so robust as those of the Long Mile specimen.

An elaborate series of intersecting ridges marks the middle part of the shaft's posterior surface (fig. 3D). These lines are presumably related to the attachments of various thigh muscles, most probably the adductores and vasti. Among living platyrrhines, equivalently strong markings on the rear aspect of the femur are seen only in taxa of large body size (e.g., *Alouatta*). In the fossil, the lines converge distally in a large projection (ap, fig. 3D). This unusual excrescence is apparently for muscle attachment as well, although nothing like it normally occurs in any known primate. It may or may not be pathological. Its tip is directed somewhat dorsomedially; mental superimposition of the femur on the hind limb of a mammal in quadrupedal posture indicates that the excrescence would have pointed toward the ischiopubic ramus and symphysis in life. This positioning implies that the outgrowth was associated with the adductor mass, which partly arises from these structures. Processes of this sort occur in several marsupials (e.g., *Metachirus, Macropus, Isoodon*), in which they are sometimes identified as "fourth trochanters" or "adductor processes" (Howell, 1941). However, true adductor processes do not seem to occur in any eutherians, even in active jumpers such as jerboas and galagos. The pectineal tubercle seen in some eutherians (e.g., *Procavia, Orycteropus*) is comparatively smaller and differently positioned.

The distal half of the diaphysis exhibits fewer muscle markings (fig. 3C, D). The medial and lateral supracondylar lines are rather feebly developed and scars for presemimembranosus (medial head of adductor magnus), plantaris, and gastrocnemius (lateral head) are small or absent. The lowermost portion of the diaphysis has a constricted appearance in medial view (fig. 3B), due to the dishing out of the suprapatellar and popliteal surfaces on opposite sides of the bone. Also evident in medial view is the conspicuous projection of the medial condyle beyond the plane of the popliteal surface, exceeding that seen in any living platyrrhine.

The fossil's distal epiphysis is both very large and anteroposteriorly compressed (i.e., shallow in relation to its transverse width) in comparison to that of living platyrrhines and even most catarrhines (fig. 5). Sizes of distal epiphyses can be compared by contrasting maximum distal width and the modified shaft-length measurement used in Ratio B (table 3). As in Ratio A, the range of sample values is narrow, but once again the group composed of *Pongo, Bradypus, Potos,* and the Jamaican fossil stands apart. All have large epiphyses relative to femoral length.

Distal epiphyseal compression can be expressed as the ratio of the oblique anteroposterior length of the lateral condyle to the maximum distal width (Ratio E, table 3; fig. 6). Extant platyrrhines range between 0.65 (*Lagothrix*) and 0.84 (*Saimiri, Aotus*). High values like those of squirrel and owl monkeys are also seen in quadrupedal lemurs (e.g., *Lemur,* 1.00), which suggests that elongated or uncompressed epiphyses are primitive for Primates (cf. Ford, 1980). (*Galago* [>1.00], however, shows a very derived condition in which lateral condyle length exceeds biepicondylar width.) Very low indices are found in suspensory and climbing mammals such as atelines, *Pongo* (0.65), *Perodicticus* (0.66), and the sloth *Bradypus* (0.59); the index for the Long Mile femur (0.58) is the lowest in the comparative set.

Ratio D (table 3; fig. 6) compares the oblique anteroposterior length of the patellar surface to the maximum distal width. Among primates, quadrupeds and energetic leapers tend to have a longer patellar surface relative to epiphyseal width than do suspensory or climbing taxa (Fleagle, 1988), although the differences are not strongly differentiated by this ratio. In the Jamaican fossil, the index is 0.42; in living platyrrhines, values range between 0.45 (*Ateles*) and 0.67 (*Saguinus*). In our nonplatyrrhine comparative sample, the lowest indices occur among the slow climbers *Pongo* (0.45) and *Bradypus* (0.38); *Perodicticus* has a higher ratio (0.53). In *Potos,* the equivalent index is 0.50.

Another ratio having possible functional implications compares the widths of the condyles as seen in posterior aspect (Ratio C, table 3). Subequal or axially symmetrical condyles tend to be found among leapers and cursorial quadrupeds, in which planar parasagittal movements of the hind limb are

TABLE 3

Femoral and Acetabular Dimensions (in millimeters) and Ratios in Extant Platyrrhines and Some Other Mammals Compared to AMNH 259900[a]

	Saguinus mystax 5 (2, 2, 1)	*Callithrix jacchus* 2 (1, 1, 0)	*Cebus apella* (5 (1, 4, 0)	*Saimiri sciureus* 5 (1, 4, 0)	*Aotus trivirgatus* 5 (1, 4, 0)	*Callicebus cupreus* 5 (2, 3, 0)	*Pithecia* spp. 4 (2, 0, 2)	*Ateles* spp. 4 (2, 0, 2)	*Brachyteles arachnoides* 1 (1, 0, 0)
Measurements[b]									
1. Maximum length	**59.1** 56.4–62.5 *2.4*	**56.3** 54.3, 58.3	**125.4** 120.2–128.3 *3.2*	**86.9** 84.3–89.9 *2.1*	**100.5** 92.5–108.2 *6.0*	**94.6** 92.1–96.4 *1.9*	**140.5** 130.5–150.9 *9.8*	**209.1** 198.4–218.2 *9.2*	**213.2**
2. Lateral condyle/ trochanteric fossa length	**54.8** 52.5–57.3 *1.9*	**52.4** 50.8, 53.9	**111.9** 103.2–115.5 *5.0*	**79.8** 76.3–82.7 *2.4*	**92.9** 86.3–100.5 *5.3*	**87.7** 86.1–89.3 *1.5*	**130.7** 119.5–144.4 *11.4*	**190.2** 184.0–200.2 *7.1*	**194.5**
3. Midshaft diameter (mesiodistal)	**3.7** 3.4–4.0 *0.3*	**3.5** 3.4, 3.6	**8.0** 7.4–8.4 *0.4*	**5.0** 4.9–5.2 *0.1*	**5.1** 4.9–5.4 *0.2*	**4.8** 4.7–5.1 *0.2*	**7.6** 7.2–8.2 *0.4*	**13.4** 12.3–14.1 *0.9*	**11.9**
4. Head diameter (anteroposterior)	**4.8** 4.5–5.2 *0.3*	**4.3** 4.2, 4.4	**10.4** 9.9–10.9 *0.4*	**6.4** 6.1–6.6 *0.2*	**7.7** 7.1–8.6 *0.7*	**7.0** 6.8–7.3 *0.2*	**10.5** 9.8–10.9 *0.5*	**18.2** 17.5–19.8 *1.1*	**17.7**
5. Medial condyle width (posterior aspect)	**2.7** 2.6–2.9 *0.2*	**2.2** 2.1–2.4	**6.0** 5.3–6.8 *0.6*	**3.6** 3.4–3.8 *0.2*	**4.1** 3.9–4.3 *0.2*	**4.2** 3.8–4.6 *0.4*	**6.3** 5.6–6.9 *0.7*	**11.7** 10.8–13.2 *1.1*	**11.1**
6. Lateral condyle width (posterior aspect)	**2.5** 2.3–2.7 *0.2*	**2.1** 2.0–2.3	**5.4** 5.0–5.6 *0.2*	**3.2** 3.1–3.4 *0.1*	**4.0** 3.7–4.2 *0.2*	**4.2** 4.1–4.4 *0.1*	**5.6** 4.7–6.1 *0.6*	**9.2** 8.7–9.9 *0.5*	**8.2**
7. Maximum distal width	**8.7** 8.5–9.1 *0.3*	**8.4** 8.3–8.5	**19.4** 18.7–20.2 *0.6*	**12.2** 12.0–12.6 *0.3*	**14.0** 13.7–14.9 *0.5*	**13.7** 13.2–14.1 *0.4*	**19.8** 18.2–21.1 *1.3*	**33.6** 31.3–35.8 *2.2*	**32.0**
8. Patellar surface length	**5.8** 5.7–6.0 *0.2*	**5.1** 5.0, 5.1	**9.5** 8.5–10.4 *0.8*	**7.8** 7.5–8.4 *0.4*	**8.6** 7.8–9.2 *0.6*	**8.4** 8.3–8.8 *0.2*	**10.9** 9.4–12.3 *1.2*	**15.2** 13.4–17.3 *1.9*	**15.5**
9. Lateral condyle length	**7.2** 6.8–7.6 *0.3*	**6.6** 6.5, 6.6	**14.4** 14.3–14.5 *0.1*	**10.2** 9.8–10.5 *0.4*	**11.7** 10.9–12.7 *0.9*	**10.6** 10.1–10.9 *0.3*	**14.2** 13.5–15.2 *0.7*	**23.6** 22.8–25.3 *1.1*	**22.4**
10. Maximum acetabular width	**5.3** 4.4–5.7 *0.3*	—	**12.4** 11.7–13.0 *0.6*	**7.9** 7.3–8.2 *0.4*	**8.9** 8.4–9.5 *0.5*	**8.1** 7.8–8.5 *0.3*	**12.1** 11.5–12.6 *0.5*	**22.2** 21.2–23.2 *1.0*	**20.8**
Ratios of means									
A. Ratio 3/2 ("robusticity")	**0.07**	**0.07**	**0.07**	**0.06**	**0.05**	**0.05**	**0.06**	**0.07**	**0.06**
B. Ratio 7/2 ("distal epiphysis size")	**0.16**	**0.16**	**0.17**	**0.15**	**0.15**	**0.16**	**0.15**	**0.18**	**0.16**
C. Ratio 6/5 ("condylar proportionality")	**0.93**	**0.96**	**0.90**	**0.89**	**0.98**	**1.00**	**0.89**	**0.79**	**0.74**
D. Ratio 8/7 ("patellar surface size")	**0.67**	**0.61**	**0.49**	**0.64**	**0.61**	**0.61**	**0.55**	**0.45**	**0.48**
E. Ratio 9/7 ("compression of distal epiphysis")	**0.83**	**0.79**	**0.74**	**0.84**	**0.84**	**0.77**	**0.72**	**0.70**	**0.70**

TABLE 3—(*Continued*)

	Lagothrix lagotricha 2 (0, 2, 0)	*Alouatta seniculus* 5 (0, 3, 2)	*Papio* spp. 5 (2, 1, 2)	*Pongo pygmaeus* 3 (1, 1, 1)	*Perodicticus potto* 5 (3, 2, 0)	*Galago senegalensis* 5 (1, 2, 2)	*Lemur fulvus* 5 (3, 2, 0)	*Bradypus variegatus* 5 (0, 2, 3)	*Potos flavus* 5 (2, 2, 1)	*Xenothrix mcgregori* AMNH 259900
Measurements[b]										
1.	**163.3** 161.3, 165.2	**155.8** 151.0–164.5 *5.6*	**243.2** 216.9–263.4 *18.7*	**263.1** 245.4–288.0	**84.7** 74.3–89.2 *6.1*	**64.9** 61.8–68.9 *3.0*	**123.5** 116.0–128.4 *4.8*	**100.9** 98.7–103.3 *2.0*	**92.2** 84.6–98.7 *6.3*	**(99.0)**[c]
2.	**150.1** 148.2, 151.9	**142.1** 136.3–150.6 *6.1*	**220.5** 193.9–225.3 *18.4*	**230.0** 212.4–252.0	**79.5** 69.7–84.3 *5.8*	**61.5** 58.3–65.2 *2.7*	**116.0** 109.7–122.9 *4.7*	**93.1** 89.8–96.2 *3.0*	**81.7** 75.7–87.2 *5.1*	**91.0**
3.	**10.0** 9.3, 10.7	**10.4** 9.2–10.9 *1.2*	**16.5** 15.0–18.4 *1.5*	**20.6** 18.3–24.5	**5.5** 4.4–6.3 *0.8*	**2.9** 2.7–3.3 *0.2*	**7.2** 7.0–7.6 *0.2*	**10.9** 10.3–11.2 *0.4*	**7.2** 6.5–8.6 *0.9*	**8.9**
4.	**14.0** 13.7, 14.3	**13.9** 12.8–14.9 *0.8*	**22.7** 20.8–25.1 *1.9*	**32.3** 29.0–37.4	**8.5** 7.5–9.6 *0.8*	**4.4** 4.1–5.0 *0.4*	**9.9** 9.6–10.2 *0.3*	**15.2** 13.7–15.9 *0.9*	**9.7** 9.2–10.2 *0.4*	—
5.	**9.0** 8.6, 9.3	**7.5** 7.0–8.4 *0.5*	**12.5** 10.4–14.4 *1.9*	**16.8** 14.3–19.8	**3.8** 3.6–4.0 *0.2*	**2.3** 2.2–2.6 *0.2*	**5.1** 4.8–5.6 *0.3*	**7.8** 6.5–8.4 *0.7*	**6.2** 5.3–6.7 *0.5*	**7.5**
6.	**7.2** 7.0, 7.4	**6.3** 5.8–7.2 *0.5*	**10.8** 9.4–11.8 *1.3*	**13.6** 12.2–16.2	**3.8** 3.6–4.0 *0.2*	**2.0** 1.8–2.5 *0.3*	**4.7** 4.5–5.3 *0.3*	**7.7** 7.2–8.3 *0.5*	**5.0** 4.5–5.3 *0.3*	**5.5**
7.	**26.7** 26.6, 26.7	**24.3** 23.1–26.5 *1.4*	**38.6** 33.2–44.1 *4.9*	**55.8** 52.1–62.5	**13.7** 12.5–15.4 *1.1*	**7.6** 7.3–8.2 *0.4*	**16.9** 16.5–17.5 *0.4*	**22.7** 21.2–24.0 *1.1*	**19.0** 16.5–20.2 *1.5*	**22.2**
8.	**12.5** 19.2, 11.9	**11.7** 10.7–13.1 *1.0*	**21.4** 17.9–23.9 *2.5*	**23.8** 19.0–29.6	**7.2** 5.9–8.4 *0.9*	**5.7** 5.5–6.0 *0.2*	**13.1** 12.8–13.5 *0.3*	**7.9** 6.9–8.8 *0.7*	**9.5** 8.5–10.3 *0.8*	**9.4**
9.	**17.4** 16.5, 18.3	**17.4** 16.2–18.8 *1.2*	**31.3** 26.9–36.4 *3.7*	**36.3** 32.7–41.7	**9.1** 8.0–10.3 *0.9*	**8.4** 7.9–9.0 *0.4*	**16.9** 16.0–17.7 *0.8*	**13.5** 11.9–14.6 *1.1*	**13.0** 11.8–14.3 *0.9*	**12.9**
10.	**17.6** 17.5–17.7	**16.7** 16.2–18.0 *0.7*	**27.6** 24.1–29.4 *2.0*	**39.9** 37.4–44.8	**9.9** 8.9–11.4 *1.1*	**5.8** 5.4–6.8 *0.6*	**11.7** 10.7–12.5 *0.7*	**17.4** 16.7–18.1 *0.7*	**11.3** 10.3–11.8 *0.7*	**14.0**
Ratios of means										
A.	**0.06**	**0.07**	**0.07**	**0.09**	**0.07**	**0.05**	**0.06**	**0.11**	**0.09**	**0.10**
B.	**0.18**	**0.17**	**0.18**	**0.24**	**0.17**	**0.12**	**0.15**	**0.24**	**0.23**	**0.24**
C.	**0.80**	**0.84**	**0.87**	**0.81**	**1.00**	**0.87**	**0.92**	**0.99**	**0.81**	**0.73**
D.	**0.47**	**0.48**	**0.55**	**0.43**	**0.53**	**0.75**	**0.78**	**0.35**	**0.50**	**0.42**
E.	**0.65**	**0.72**	**0.81**	**0.65**	**0.66**	**1.11**	**1.00**	**0.59**	**0.68**	**0.58**

[a] All specimens are wild-caught adults in AMNH collections. The numbers below each taxon name are sample size and (in parentheses) sample sex distribution (male, female, unspecified) as recorded on museum tickets, for measurements 1–9. For measurement 10, sample sizes are different only for *Perodicticus* and *Potos* (N = 4). Values in boldface are means (except in cases where N = 1), values in roman are ranges, and values in italics represent standard deviations.

[b] Measurements: **1.** From proximal surface of head to farthest distal point on condyles (plane usually oblique to long axis of shaft). **2.** From distal margin of trochanteric fossa to distalmost point on lateral condyle. **3.** Taken at approximate middle of shaft, on a plane parallel to distal surface of condyles (determined by resting condyles on a surface). **4.** Taken perpendicular to long axis of shaft. **5.** Minimum breadth of posterior surface, taken in upper one-half or one-third of condyle (cf. fig. 5). **6.** Measured in same plane as **5**; may not be minimum. **7.** Maximum breadth across distal end, regardless of position of epicondyles; taken parallel to condyles resting on a surface. **8.** With one arm of caliper on middle of distal (inferior) margin of patellar surface, maximum oblique distance to middle of proximal (superior) margin of same surface (cf. fig. 6). **9.** With one arm of caliper on lateral lip of patellar surface, maximum oblique distance to proximal summit of lateral condyle (cf. fig. 6). **10.** Maximum inside diameter of acetabulum (not including thickness of rim); cf. Schultz (1969).

[c] Linear regression of measurement **1** on **2** for a modern platyrrhine sample (N = 41) yields a maximum length estimate of 99.0 mm for AMNH 259900 ($a = 1.095$, $b = -0.625$; $r = 0.99$).

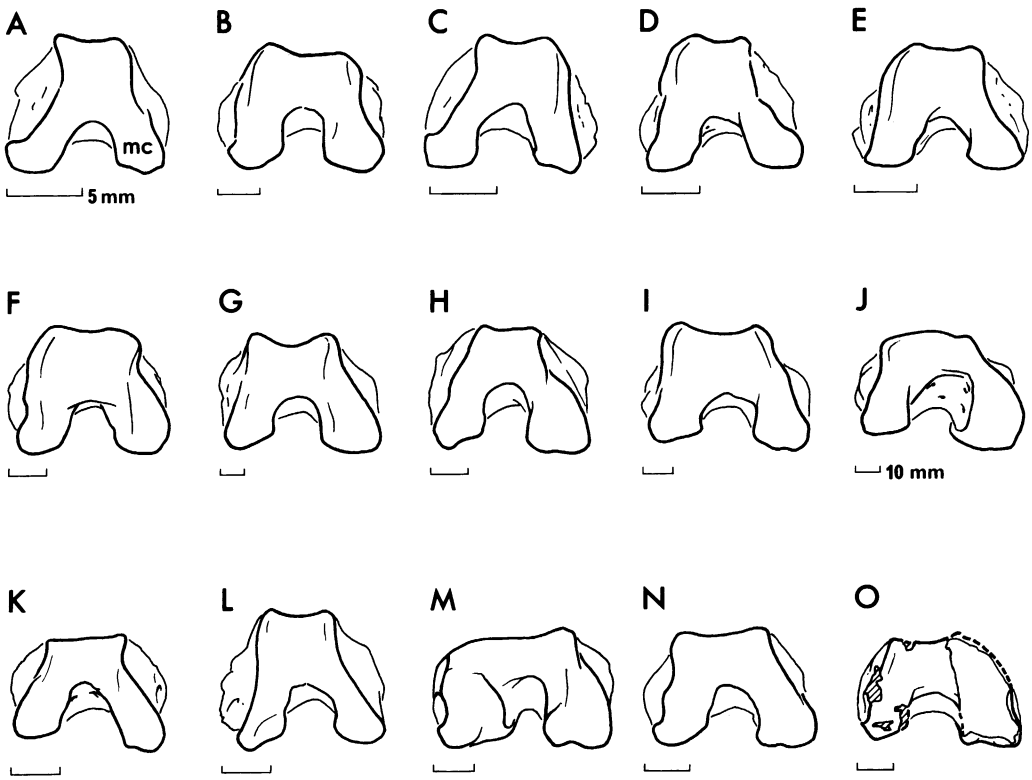
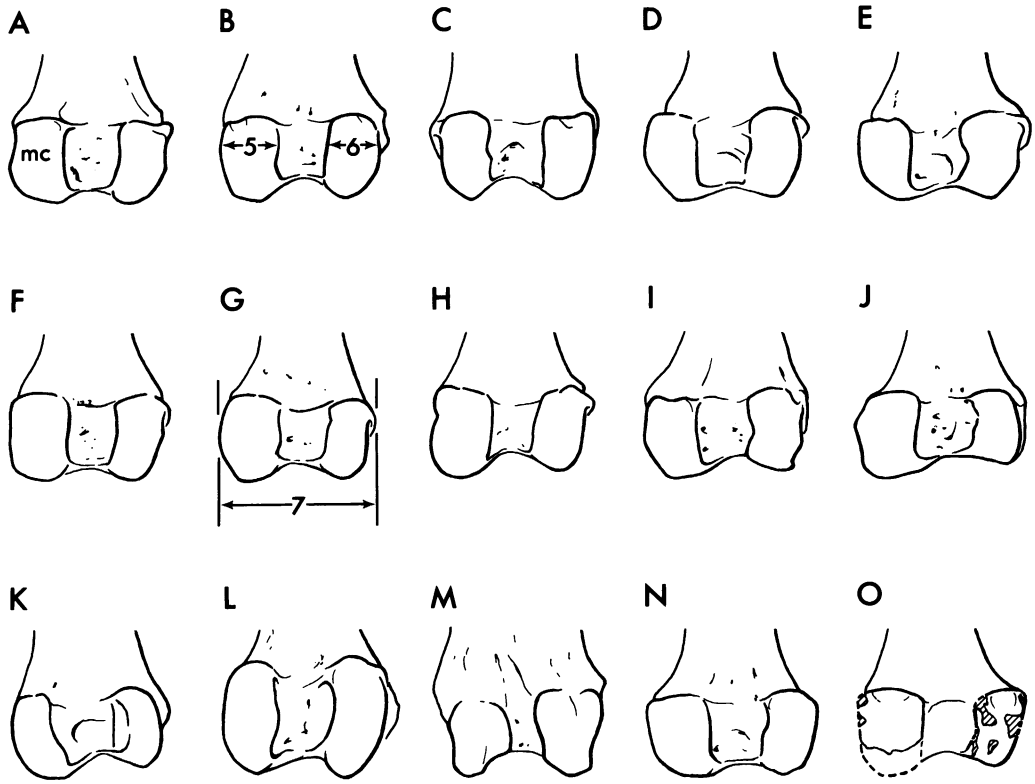


Fig. 5. Distal (**above**) and posterior (**opposite page**) aspects of distal articular surface of right femur. **A.** *Callithrix argentata,* AMNH 184689. **B.** *Cebus apella,* AMNH 211579. **C.** *Saimiri sciureus,* AMNH 211627. **D.** *Aotus trivirgatus,* AMNH 187963. **E.** *Callicebus moloch,* AMNH 136217. **F.** *Chiropotes satanus,* AMNH 95760. **G.** *Brachyteles arachnoides,* AMNH 245700. **H.** *Lagothrix lagotricha,* AMNH 201310. **I.** *Alouatta seniculus,* AMNH 48119. **J.** *Pongo pygmaeus,* AMNH 28252. **K.** *Perodicticus potto,*

emphasized (Fleagle, 1976; Jenkins and Camazine, 1977; see also Tardieu, 1983). Asymmetrical condyles are common in arboreal quadrupeds and climbers, in which the knee is frequently held in an adducted or abducted posture.

Femoral condyles are complicated shapes, and width measurements for Ratio C will vary considerably depending on where the calipers are placed. Our measurement was taken in the upper half of each posterior condylar surface, since this is the region in which width differences between condyles (if any) tend to be marked. The chief contrast (fig. 5) is between the majority of taxa in which the two condyles are essentially subequal, and those in which there is a considerable disparity (>20%). At 0.73, the fossil nearly matches the lowest values recorded for this ratio in Platyrrhini (0.74, in *Brachyteles*). *Pongo,* in which the disproportion between condyles is very obvious (fig. 5J), exhibits a value of 0.75. However, there is no consistency within the slow climbing group because both *Bradypus* and *Perodicticus* display high values. In *Potos* the index is 0.81, which is moderately low.

The upper third of the medial condyle's posterior articular surface bears a concave depression (figs. 3B, 5O). A much smaller facet is found on the proximal summit of the lateral condyle. These fossae presumably accommodated large fabellae (sesamoids in the heads of gastrocnemius); similar but shallower surfaces are found in many platyrrhines (and many other mammals) in which fabellae are known to occur.



AMNH 52682. **L.** *Lemur fulvus,* AMNH 100528. **M.** *Bradypus variegatus,* AMNH 42838. **N.** *Potos flavus,* AMNH 62093. **O.** AMNH 259900 (attributed to *Xenothrix mcgregori*). Each specimen drawn at approximately the same size to facilitate comparisons; actual scales indicated beneath specimens (all scale bars = 5 mm, except in **J**). In **O,** small imperfections are filled in with hatchure; estimated outlines of larger defects are indicated by dashed lines. Measurements 5–7 (in **B** and **G**) are defined in table 3.

The patellar surface on the anterior aspect of the fossil must have originally been fairly wide, but much of its medial portion is gone (fig. 4C). It is therefore difficult to determine the orientation of the patellar ridges, although there is no reason to suspect that they were anything other than subparallel. It is somewhat clearer that they were comparatively widely separated, and it is certain that the intact lateral patellar ridge was low (fig. 5O). Among primates, a prominent lateral patellar ridge is characteristic of species in which the vastus lateralis is comparatively large (leapers, bipeds). During locomotion, the ridge presumably resists the tendency of the vastus lateralis to laterally displace the patella and therewith the leg (Fleagle, 1976, 1988). Patellar surfaces and ridges vary widely in size and definition in platyrrhine fam-

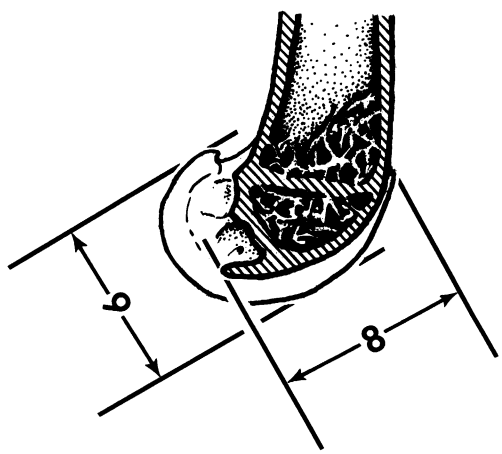


Fig. 6. Parasagittal section of distal end of left femur of a representative platyrrhine, to illustrate method for taking measurements 8 and 9 (table 3).

TABLE 4

Body Weight Estimates for *Xenothrix* Based on Femoral Cortical Cross-Section Method of Ruff (1987)

1. Cross-section measurements of AMNH 259900 (in millimeters), taken at 50% femoral length

External diameter		Cortical bone thickness		Area (in mm^2)	
Anteroposterior	8.96	Anterior	1.25	MA (medullary area)	35.09
Mediolateral	9.61	Medial	1.35	TA (subperiosteal/total area)	67.64
		Posterior	1.15	CA (cortical area, TA − MA)	32.54
		Lateral	1.45		

2. Ruff's (1987) regression expressions for estimating body weight (BW)

Expression derived from total primate sample ($r^2 = 0.988$):	Expression derived from nonhuman primate sample ($r^2 = 0.992$):
$\log_{10}BW1 = 1.291(\log_{10}CA) - 1.453$	$\log_{10}BW2 = 1.312 - 1.488(\log_{10}CA)$

3. Body weight estimates for AMNH 259900

BW1 = 3.16 kg	BW2 = 3.14 kg

ilies, although on the whole callitrichids display comparatively narrower anterior patellar surfaces than do most cebids or atelids (fig. 5). Although the anterior patellar surface is relatively shallow in AMNH 259900, it is no more so than in many other platyrrhines when viewed in distal profile (fig. 5).

It is appropriate to note here that the Long Mile femur also displays some resemblances to femora of Eocene adapids (e.g., compressed distal epiphysis, weak patellar ridges, broad and shallow patellar articular surface; Dagosto, 1983). On the other hand, the shaft of the Long Mile femur is considerably more robust than in either *Adapis* or *Leptadapis,* and both of these early strepsirhines lack the sculpture seen on its posterior aspect. Nor are there any meaningful correspondences in dentition between adapids (or omomyids) and *Xenothrix.* These facts, combined with the obviously wide temporal gulf between these taxa, suggest to us that any resemblances are simply the result of convergence among species adapted for nonleaping, slow-moving arboreal quadrupedalism.

We used Ruff's (1987) expressions for log body weight regressed against log femoral cortical cross-sectional area in living primates to estimate the body size of the animal represented by the Long Mile femur. Cortical measurements for the fossil were derived radiographically, using the technique of Biknevicius (1990). Ruff's two regressions (for different samples of primates) yield, in this case, very similar results of slightly more than 3 kg (table 4). Estimates derived from bracket comparisons ("narrow" allometry) are in line with this value. The fossil's midshaft diameter falls midway between the averages for *Cebus apella* and *Lagothrix lagotricha* (table 3). Mean combined-sex body weights in these species are 2.6 kg and 7.3 kg, respectively (data of Jungers, 1985), for a grand "mean" of 5.0 kg. These species are moderately dimorphic; female means are 1.9 kg and 5.7 kg (grand "mean", 3.8 kg). Interestingly, the upper range for femoral midshaft diameter in *Potos flavus* almost overlaps the value for AMNH 259900 (table 3)—and kinkajous have a reported body weight of 1.4–2.7 kg (Walker et al., 1975). On the basis of this information, we conclude that a body weight of 2–4 kg is intuitively probable for the Long Mile species.

In summary, the functionally important features of the Long Mile femur (large size of distal end, compression of distal epiphysis, broad anterior patellar surface with low lateral lip) are ones that generally characterize slow quadrupedal/climbing primates and distinguish them from either leapers or cursorial ground quadrupeds. The femur does not meaningfully resemble the femur of any known nonprimate of the Neotropics, with the egregious exception of *Potos flavus* and, to a much lesser degree, pilosans. The resemblances to sloths are surely convergences, and those to kinkajous are not so great that we feel justified in allocating the Long Mile femur to a group not otherwise known from Jamaica (but see Discussion). In view of the place of its discovery and apparent associa-

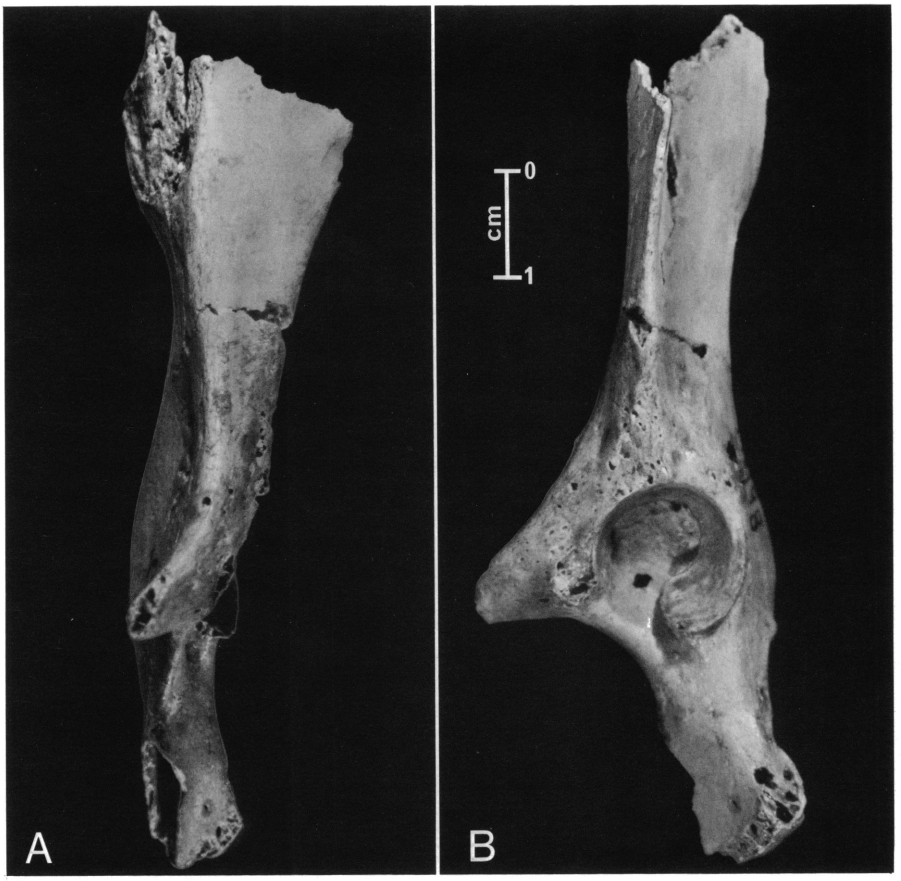


Fig. 7. Os coxae (AMNH 259904) attributed to *Xenothrix mcgregori,* Anthony collection, Long Mile Cave. **A.** Oblique ventral. **B.** Lateral.

tion with the decidedly primatelike os coxae (see below), AMNH 259900 is best allocated to the hypodigm of *Xenothrix mcgregori.*

We purposely frame our conclusion in this way because there are some important gaps in our analysis that we cannot fill with the material at hand. Thus, while we think that the Long Mile femur is that of a primate, we cannot cite any trait that marks it as unquestionably platyrrhine. For the present, its allocation to Platyrrhini will have to rely on inferences from biogeography, not morphology—a point that we feel applies with equal force to the *Xenothrix* jaw. (Allocational difficulties of this kind are not without precedent in primate paleontology. We are particularly reminded of early confusion surrounding the bradypodidlike femur of the Malagasy subfossil indriid *Palaeopropithecus* [cf. Grandidier, 1901; Lamberton, 1947]. This story is usually cited as a cautionary against making sweeping taxonomic inferences from single elements, but it might be used equally well to make the point that one ought not to expect that recently extinct animals will always differ trivially from their living relatives.)

Nor can we reasonably exclude from consideration Hershkovitz' (1988) suggestion that the Coco Ree femur is actually that of *Xenothrix.* Morphology is on Hershkovitz' side, of course, because the Coco Ree specimen is typically platyrrhine. But if the Long Mile femur is not that of *Xenothrix,* what is it?

Os Coxae

The partial left os coxae (AMNH 259904) in the Long Mile collection is definitely anthropoid rather than strepsirhine- or *Potos*-like in aspect (figs. 7, 8). However, in parallel

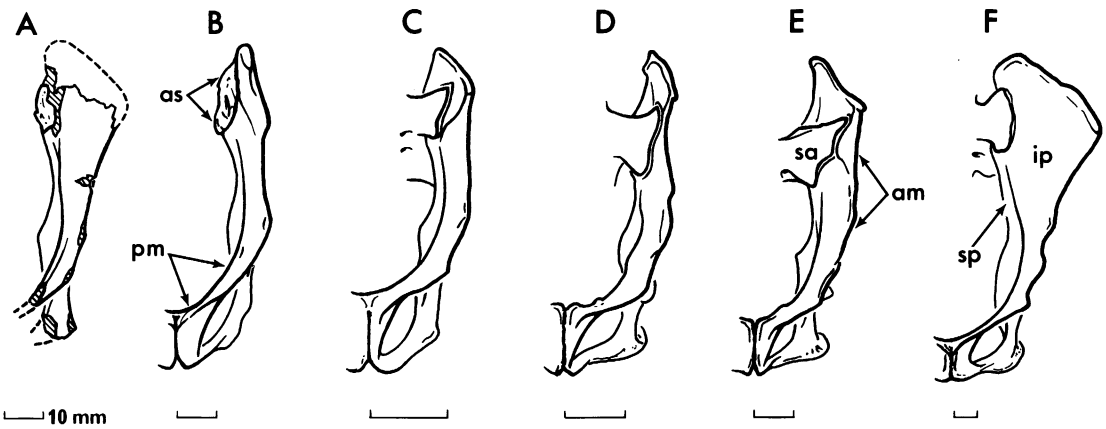


Fig. 8. Oblique ventral (**above**) and lateral (**opposite page**) aspects of left os coxae. **A.** AMNH 259904 (attributed to *Xenothrix mcgregori*). **B.** *Potos flavus,* AMNH 62093. **C.** *Callithrix argentata,* AMNH 184689. **D.** *Callicebus moloch,* AMNH 211488. **E.** *Pithecia hirsuta,* AMNH 248723. **F.** *Brachyteles arachnoides,* AMNH 245700. **Above,** drawing viewpoint is perpendicular to iliac planum (ip); on **opposite page,** viewpoint is perpendicular to midsagittal plane (estimated in case of **A**). Each specimen drawn at

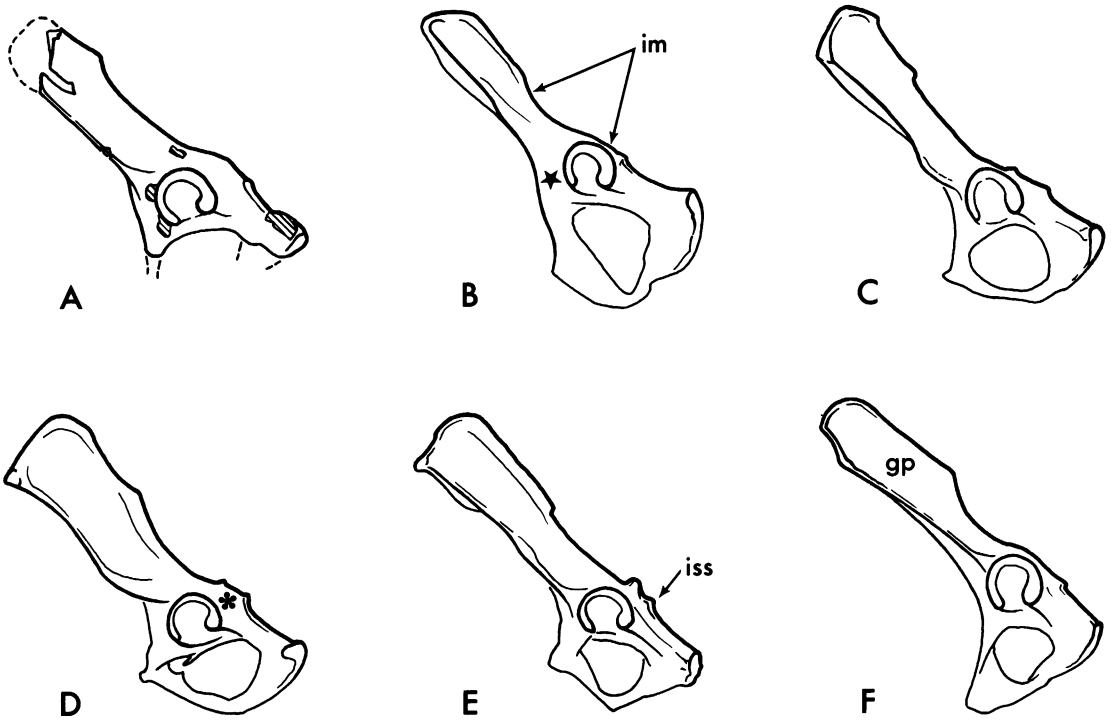
with the primate femur from Long Mile, the coxal fragment exhibits a suite of derived traits that distinguish it from its counterparts in all known platyrrhines. Some apomorphies, such as the breadth of the iliac surface, are replicated in some platyrrhines of very large body size (*Brachyteles*); others, such as the width of the dorsal acetabular margin, recall quadrupedal cercopithecoids.

The coxal fragment consists of the acetabular region and contiguous portions of the ilium, ischium, and pubis (fig. 7). The ischial tuberosity is broken and there are defects in the acetabular rim, the acetabular fossa, and the gluteal and iliac surfaces. No portion of the pubic symphysis is preserved, and the full size of the iliac blade cannot be determined from existing remains. The element's longest dimension (caudal surface of the ischium to cranialmost point on the preserved part of the ilium) is approximately 80 mm. Although it is not possible to estimate precisely how much bone has been lost from the blade, it is reasonable to believe that some 5–10 mm are missing (fig. 8A). This would place the os coxae from Long Mile in the range of small species of *Cebus* and *Chiropotes,* at least for this dimension.

The acetabulum of AMNH 259904 is large but shallow (fig. 7; table 3). Femoral heads as large as those of *Cacajao* (mean, 12.5 mm; N = 3) and *Chiropotes* (mean, 11.5 mm; N = 3) can easily be accommodated within it, suggesting that the femur that articulated with this os coxae had a head comparable to that of middle-sized living platyrrhines.

The iliac portion of the fossil is prismatic in form and has three well-defined surfaces—the gluteal, sacral, and iliac planes. The iliac and gluteal planes are separated by a very prominent acetabular margin (figs. 7, 8A). Immediately above the acetabular rim is a small depression, for either the origin of rectus femoris, part of the iliofemoral ligament, or both. There is no indication of an anterior inferior iliac spine, prominent in many platyrrhines (e.g., fig. 8C, D), although the relevant area is abraded on the fossil. The sacral plane is gently concave; it is bounded caudally by an eminence corresponding to the deepest part of the acetabular fossa. The plateau on which the auricular surface was situated is present, but most of the articular facet for the sacrum has been destroyed and its original size cannot be gauged (figs. 7, 8).

One of the most distinctive features of the Long Mile os coxae is the great width, ventromedial orientation, and craniad flare of the iliac blade (fig. 8A). The majority of platyrrhines exhibit rather narrow iliac planes, defined by pubic and acetabular borders that are either subparallel or actually converge in a cranial direction (e.g., fig. 8C, D). Well-developed iliac surfaces with diverging bor-



approximately the same size to facilitate comparisons; actual scales indicated beneath specimens (all scale bars = 10 mm). Dashed iliac border in **A** represents an estimate of the amount of bone lost from the pelvic blade; short dashes indicate widths of pubic and ischial rami at their respective origins. Ventral (star, **B**) and dorsal (asterisk, **D**) acetabular rims are indicated.

ders are seen only in larger species (Sigmon and Farslow, 1986; Fleagle and Kay, 1987). Despite the fact that the uppermost part of its blade is missing, the Long Mile os coxae clearly possessed highly divergent borders. If size is ignored, AMNH 259904 more closely resembles the os coxae of *Brachyteles* (fig. 8F) than that of any other ceboid. Callitrichids, by contrast, exhibit exceptionally narrow iliac plana (fig. 8C). *Potos* has a slightly larger iliac surface than do other procyonids, and megalonychids possess expanded ilia (Anthony, 1918), but the ossa coxae of kinkajous and Antillean sloths are otherwise modified in ways not exhibited by the Long Mile specimen. Caviomorphs and Antillean insectivores have narrow blades.

The body of the ischium of AMNH 259904 is wide but short (fig. 7). The ischiopubic ramus, broken near its origin from the body, also appears to have been wide. The sciatic margin bears a low eminence equivalent to the ischial spine, which helps to demarcate the cranial end of the area homologous with the lesser sciatic notch of *Homo*. In the fossil and in living ceboids this area is occupied by a broad, smoothly rounded platform (for the tendon of obturator internus) whose arc of curvature extends from the ventral to the dorsal aspect of the ischium. The lateral surface of this smoothly rounded area terminates in a raised ridge, which is presumably related to attachments for limb musculature (gemelli and quadratus femoris).

The pubis is only partly preserved. At its origin from the acetabular region it is wide, but the ramal portion is notably tapered and gracile. The ramus juts from the coxal body at a wide angle, in typical anthropoid fashion. In most other mammals, arboreal ones included (e.g., *Potos*, fig. 8B), the ramus is more sharply inclined.

Fleagle and Simons (1979) correlated the relative widths of the ventral and dorsal rims of the acetabulum with major locomotor differences in higher primates: species that prac-

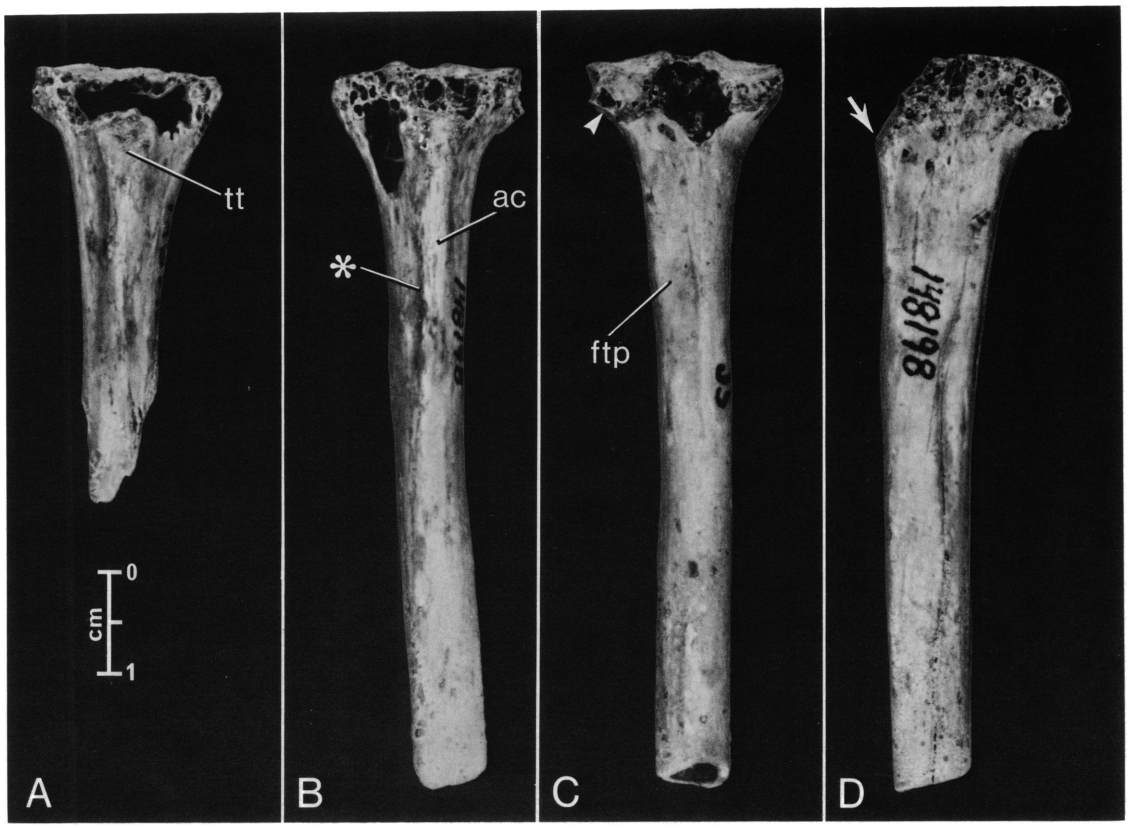


Fig. 9. Tibiae attributed to *Xenothrix mcgregori,* Anthony Collection, Long Mile Cave. **A.** AMNH 259902, anterior aspect. **B, C, D.** AMNH 259903, anterior, posterior, and lateral aspects (to same scale). Asterisk in **B** marks insertion of sartorius, gracilis, and semimembranosus; pointer in **C** lies on facet for head of fibula; and white arrow in **D** draws attention to projection and high proximal position of tibial tuberosity.

tice limb suspension have substantially equal rims, while more pronograde forms have thicker dorsal rims. In view of the broad, atelinelike iliac surface of AMNH 259904, it might be assumed that its rim ratio (table 2) would be similar to that of spider monkeys. However, examination of Schultz' (1969) data reveals that the fossil's ratio of 0.61 is lower than that of any extant platyrrhine (lowest values: 0.66–0.68 in female *Cebus* and *Calalithrix*) and most catarrhines (lowest values: 0.55–0.63 in female *Macaca, Papio, Cercocebus, Cercopithecus,* and *Presbytis*). It should be noted that Schultz' (1969) data also indicate the existence of a rather marked sexual difference in this ratio, with values for males being as much as 10–20 points higher than those for females of the same species. Body size factors probably play some sort of role, because *Pongo* has a rather low ratio (0.71–0.84) but *Hylobates* has a high one (0.97–0.99). However, this is not a full explanation, because all strepsirhines express very high values (1.30–1.70), whatever their individual locomotor preferences. Among the nonprimates studied by us, *Potos* has a notably higher value (mean, 1.21; N = 5) than the more terrestrial *Nasua* (mean, 0.84; N = 5).

While the functional correlates of the fossil's low acetabular-margin index are obscure, the index value and the wide iliac blade are nearly the only significant resemblances to cercopithecoids. The expanded ischial tuberosity of Old World monkeys is obviously absent, and the fossil lacks the very stout, pillarlike ischial body seen in these primates.

Since the ilium is incomplete, it is not possible to utilize Schultz' (1969) ilium/ischium length ratio. Fleagle and Simons (1979), faced with a similar problem in describing fragmentary ossa coxae of parapithecids, calculated a modified ratio using lower ilium length. They found that living ceboids vary between 0.93 and 1.75. Atelines occupy positions in the upper end of this range. By contrast, most cercopthecoid generic averages fall within a narrow range at the low end of the scale (1.00–1.20). These figures suggest that suspensory primates tend to have relatively longer lower ilia than do primates which do not engage in a great deal of limb suspension. Somewhat surprisingly, the ratio for AMNH 259904 is quite low (1.05).

In size and robusticity the Long Mile os coxae is a good match for the primate femur from the same locality. However, locomotor correlates are at present unclear: the expanded iliac planum is certainly consistent with slow quadrupedalism or climbing (as also suggested by features of the femur), but the acetabular-margin and modified ilium/ischium ratios are not.

TIBIAE

The two partial tibiae (AMNH 259902, 259903) in the Long Mile series are rather nondescript (fig. 9). Each fossil consists of the proximal articular end plus a portion of the shaft; both are severely damaged, but enough remains to be certain that they do not belong to *Geocapromys*. The right tibia agrees in size with the femur described above, and despite their incompleteness the two bones can be satisfactorily articulated in the close-packed position (midflexion). They are therefore likely to represent the same species and perhaps the same animal.

The proximal articular surfaces of both tibiae are incomplete, but by combining tracings of each it was possible to recreate the general appearance of the original surface (fig. 10). The medial condylar facet was clearly wider and longer than the lateral, as would be expected from the conformation of the distal articular surface of AMNH 259900 (fig. 5O).

The presence of a proximal fibular joint surface under the lateral condyle establishes that the proximal end of the fibula was not coossified with the tibia (fig. 9C)—an important distinction from *Geocapromys,* in which tibiofibular fusion normally takes place. Although neither shaft is complete, the interosseous border of the longer specimen (AMNH 259903) lacks a diaphyseal facet for the fibula. Thus it is reasonable to infer that the diaphyses of the leg bones were neither fused nor closely appressed. In all these features, the Long Mile leg bones are simply primitive.

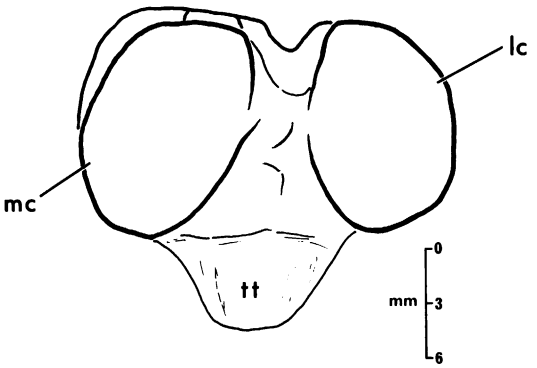


Fig. 10. Reconstruction based on proximal articular surfaces of Long Mile tibiae (AMNH 259902, 259903), to show relative size and proportions of condyles. The intercondylar area is damaged in both specimens, but was probably of low relief.

In posterior and anterior profile the shafts of the Long Mile specimens display a slight medial convexity; in lateral and medial profile their anterior borders are practically straight distal to the tibial tuberosity. The diaphyseal cross sections exposed by fracture are subcircular. In these features the fossils resemble some larger-bodied platyrrhines (*Alouatta, Cacajao,* and atelins) but differ from Antillean insectivores and rodents (including *Geocapromys*), in which the diaphysis tends to be bowed, compressed mediolaterally, or both.

Muscular markings are strong only on the anterior surface of the diaphysis. The tuberosity (fig. 9D) is rather prominent for a platyrrhine tibia and is located more proximally than in most New World monkeys (but agrees with *Potos* in this regard). This eminence is continued distally as a sharp ridge (anterior crest) for about 2 cm down the front of the shaft. The medial relief of this crest is exag-

gerated by a deep muscle scar, evidently for the combined insertions of sartorius, gracilis, and semitendinosus (fig. 9B). On the posterior surface (fig. 8C) there is a moderately excavated fossa, probably for tibialis posterior. *Alouatta* expresses most of these features to about the same degree, although in relative terms its tibial tuberosity is somewhat less powerfully built. By contrast, callitrichids express a low, distally situated tibial tuberosity and lack prominent muscular scars (although the latter may be size-related).

Unfortunately, the primate tibial fragment from Hispaniola (USNM 254682, "Ceboid M"; Ford, 1986b) and the two specimens from Long Mile have no landmarks in common, making comparison difficult. However, it may be noted that the anteroposterior shaft diameters of Ceboid M (cast) and AMNH 259903, measured as close as possible to their broken ends, are respectively 8.8 and 7.5 mm. Their mediolateral diameters are virtually the same (7.1 and 7.0 mm). This may imply that the monkeys were of similar body size, but does not justify any conclusions about relationship.

Few functional implications can be drawn from the incomplete Long Mile tibiae. The protuberance of the tibial tuberosity, the depth of the scar for semitendinosus and related muscles, and the apparently large size of the fabellae in the heads of gastrocnemius (as judged from the Long Mile femur) are consistent with powerful extension and flexion of the leg at the knee. However, assuming that the association of the femur and tibiae is good, the evident shortness and robusticity of the hind limb long bones do not indicate exceptional leaping abilities.

Humeri

There are three noncapromyid humeri in the Long Mile sample (figs. 11, 12). The two smaller humeri are morphologically and metrically similar, but far too small to belong with any of the postcranial bones considered above (including the Coco Ree and Sheep Pen specimens). Although they resemble the humeri of unspecialized insectivores and carnivores in some respects, they do not precisely match those of any species in our comparative sample (which includes *Herpestes auropunctatus,* the introduced mongoose). In short, we do not know what mammalian group these specimens represent and refrain from assigning them to a specific higher taxon.

The small right humerus (AMNH 259905) is slightly more complete than the left (AMNH 259906), although both lack heads and the right element retains only a small section of the distal articular end (fig. 11A, B). They may be conveniently described together.

Relative to its apparent length, the shaft is quite robust, especially in its upper half. In lateral view the posterior surface is essentially straight, but the anterior aspect is distorted by a lengthy and smoothly rounded deltopectoral eminence that is unlike the sharp crest of most platyrrhines. In this regard the humeral shaft bears a notable resemblance to that of the extinct West Indian soricomorph *Nesophontes* (cf. Anthony, 1918), although the largest known species in this genus had a humerus less than half the apparent size of the Long Mile specimens.

Among living ceboids, the lateral border of the humerus tends to be relatively straight in its distal third. In the small humeri from Long Mile, the profile of the lateral border is notably concave because the lateral supracondylar ridge is insignificant and there is accordingly no brachialis flange (= enlarged lateral supracondylar ridge) of the sort found in medium- and large-sized cebids and many climbing mammals (including *Potos*).

A distinctive feature of the medial border of the fossil humeri is a capacious entepicondylar foramen. Although many platyrrhines exhibit this feature, it is by no means restricted to them and is best regarded as a primitive eutherian characteristic.

The medial epicondyle is not preserved, but the great thickness of bone in its stump suggests that this process must have been large. There is a large dorsal epitrochlear fossa for attachment of the ulnar collateral ligament (fig. 11B). This feature is small or absent in arboreal caviomorphs, sloths, and Antillean insectivores. Unfortunately, nothing is left of the capitulum in AMNH 259905, although most of the posterior half of the trochlea is preserved. The olecranon fossa is deep and capacious, which implies that the olecranon process of the ulna must have been

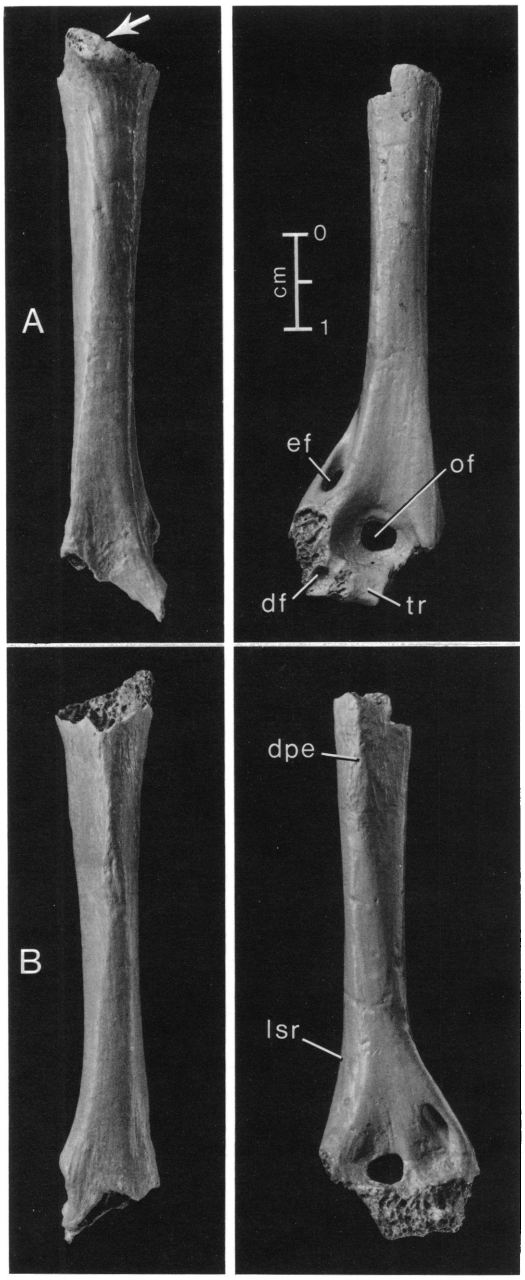


Fig. 11. Small unattributed humeri, Anthony Collection, Long Mile Cave. **A.** Posterior aspects of AMNH 259906 (**left**) and 259905 (**right**). **B.** Anterior aspects of same specimens (to same scale). White arrow in **A** points to apparent metaphyseal surface (for proximal epiphysis).

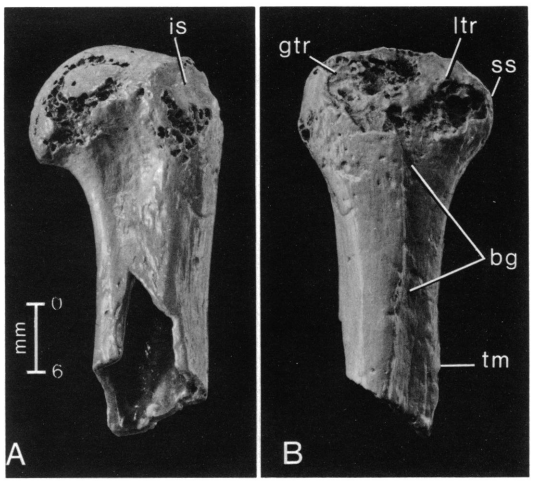


Fig. 12. Large unattributed right humerus (AMNH 259901), Anthony Collection, Long Mile Cave. **A.** Lateral. **B.** Posterior.

large and projecting. It is possible but doubtful that the defect in the fossa's floor is natural.

Only the distal part of the bicipital groove is preserved in either specimen; it is broad and very shallow. The proximal extremity of the right humerus bears what appears to be part of the metaphyseal surface, which suggests that the humeral head was not fully fused to its shaft at the time of death. However, morphological departures from the larger humerus (AMNH 259901) are so great that we can confidently reject the hypothesis that the differences are ontogenetic and that all three humeri should be allocated to one species.

AMNH 259901 (fig. 12) is equally difficult to place systematically. In size, it is large enough to be provisionally associated with any one of the allegedly primate femora now known from Jamaica. However, in most of its preserved features it is not at all primate-like. In profile the specimen's head may be described as rounded but not spherical. The head index (Fleagle and Simons, 1979) is 0.88, which is smaller than that of suspensory monkeys such as *Ateles,* but is comparable to that of *Alouatta* (0.84) and *Cebus* (0.87). On the posterior surface, the neck of the humerus is indented by a pair of fossae of uncertain significance. The deltopectoral crest is not represented on the preserved part of the humerus.

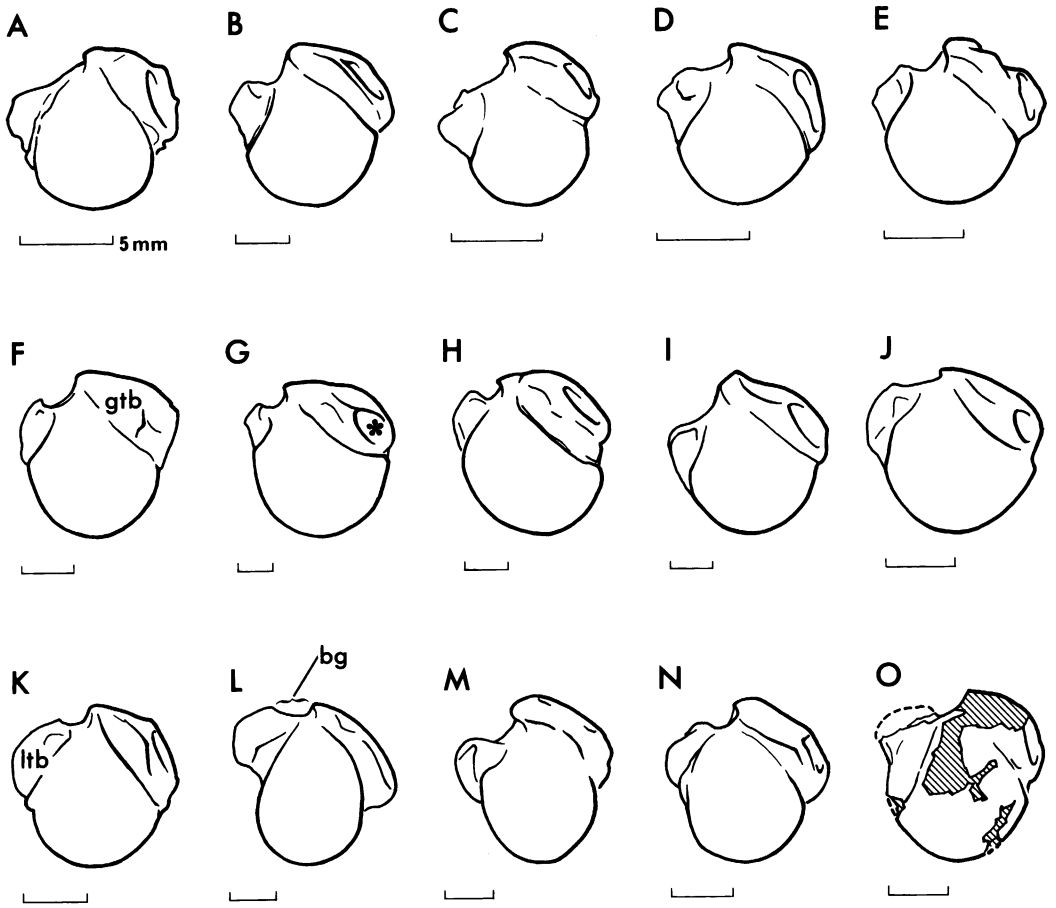


Fig. 13. Proximal articular surface of right humerus. **A.** *Callithrix argentata,* AMNH 184689. **B.** *Cebus apella,* AMNH 211579. **C.** *Saimiri sciureus,* AMNH 211627. **D.** *Aotus trivirgatus,* AMNH 187963. **E.** *Callicebus moloch,* AMNH 211488. **F.** *Chiropotes satanus,* AMNH 96123. **G.** *Brachyteles arachnoides,* AMNH 245700. **H.** *Lagothrix lagotricha,* AMNH 201310. **I.** *Alouatta seniculus,* AMNH 48119. **J.** *Perodicticus potto,* AMNH 52682. **K.** *Lemur fulvus,* AMNH 100528. **L.** *Bradypus variegatus,* AMNH 42838. **M.** *Potos flavus,* AMNH 62093. **N.** *Geocapromys brownii,* AMNH 45156. **O.** AMNH 259901 (unattributed). Heads drawn with epicondyles oriented in same plane (as viewed here, parallel to bottom of page). Anterior surface toward top of page. Asterisk in **G,** fossa for infraspinatus m. Each specimen drawn at approximately the same size to facilitate comparisons; actual scales indicated beneath specimens (all scale bars = 5 mm).

Anteriorly, the bicipital groove has distinct margins, is comparatively deep, and displays no tendency to twist across the shaft. The greater and lesser tuberosities are abraded, but they would clearly have been rather prominent in the intact state (Fig. 13O). The lesser tuberosity was probably moderately projecting, but like the greater tuberosity it did not extend proximally above the humeral head. On the lesser tuberosity's medial surface there is a deep scar for subscapularis. Distally, the lesser tuberosity grades into a prominent crest, part of which would have borne the teres major insertion. The positioning of the tuberosities is not like that of highly arboreal primates; in particular, the lesser tuberosity is more anteromedial in position than in living platyrrhines (fig. 13).

In several respects AMNH 259901 is distinctly like the humerus of some caviomorphs, although it is too large to belong to *Geocapromys* and too small to belong to *Cli-*

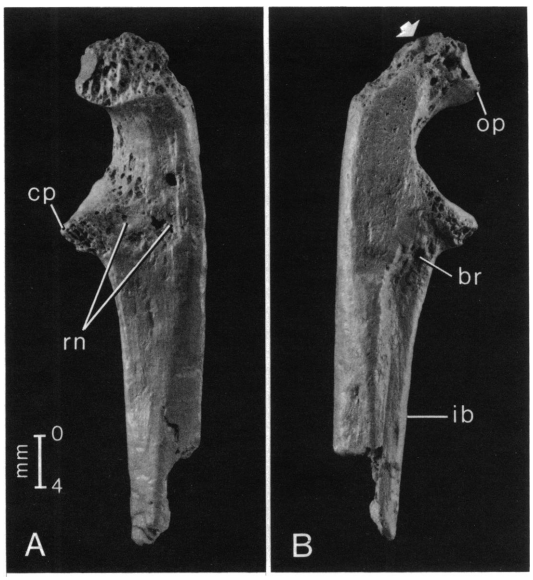


Fig. 14. Unattributed left ulna (AMNH 259907), Anthony Collection, Long Mile Cave. **A.** Ventral. **B.** Lateral. White arrow in **B** points to apparent metaphyseal surface (for proximal epiphysis).

domys, the giant heptaxodontid of Jamaica (MacPhee, 1984). Other than size, its most obvious difference from *Geocapromys* is the conformation of the head (fig. 13N, O) and the depth and definition of the bicipital groove as seen from the posterior aspect. However, deep grooves are found in some other caviomorph families (e.g., Erethizontidae), as is the combination of semirounded head, widely separated tuberosities, and deep excavation of the neck. There is certainly very little to indicate profound adaptations for arm suspension, at least in preserved parts of the specimen.

Useful comparisons of AMNH 259901 to Eocene and Recent strepsirhines are precluded by the absence of most of the shaft and the distal end in the Long Mile specimen (cf. Dagosto, 1983).

One of our reviewers asked why, if we were willing to grant that the Long Mile femur can be allocated to *Xenothrix* despite its generally nonprimate aspect, we did not make the same inference for the equally unusual large humerus. The answer is that in at least a few features, such as the flaring lesser trochanter, the femur is arguably more like that of a primate than anything else. The preserved part of the humerus, by contrast, lacks such distinctive traits, and for the present we feel that the better course is to leave it in the unattributed category.

Ulna

The Long Mile left ulna (AMNH 259907) consists of the proximal end and a small portion of the shaft (fig. 14). Although this specimen was boxed with ulnae referable to *Geocapromys,* it differs in a number of morphological details from the hutia ulna and clearly belongs to some other taxon. Unfortunately, AMNH 259907 was heavily and somewhat ineptly cleaned; in several areas the outermost layers of cortical bone have been scraped off, so that even apparently intact surfaces have been stripped of surface detail.

The olecranon process is partly preserved, but the processus muscularis for triceps is missing. In this case loss may be due to the separation of the epiphysis after deposition; proximally, there is a rugose area that seems to have been part of a metaphyseal surface.

Both the olecranon and the coronoid are robustly built and projecting, and help to define a deep trochlear notch that completes the better part of a half-circle. The size and depth of the notch are relatively much greater than in *Geocapromys brownii.* Bone has been lost from the coronoid's rims, and it is impossible to say how broad the original articular area for the trochlea was. The radial notch is also abraded, but it appears to have been shallow and subvertical in its orientation. Movements related to pronation and supination were presumably unrestricted.

The remarkably broad posterior surface of AMNH 259907 is approximately twice as thick as the equivalent surface on the ulna of *Geocapromys,* and is much straighter in lateral profile. Distinct crests and fossae for muscular origins (e.g., extensors of hand, deep digital flexor) appear to be lacking from the upper end of the shaft, but this appearance is probably due to the scraping away of surface relief during preparation.

On the medial surface beneath the coronoid process there is a deep scar for the origin of brachialis, and the preserved part of the interosseous border is sharp.

Although the Long Mile ulna seems somewhat large for association with the small humeri, the disparity is not so great as to exclude the possibility (especially in view of the fact that both AMNH 259906 and 259907 may be subadult). The large size of the trochlear notch is in keeping with the (inferred) large size of the distal articular surfaces of the small Long Mile humeri. The robusticity of the processes defining the trochlear notch imply a well-braced elbow. These adaptations do not point to any single functional complex, although some form of scansorial or quadrupedal activity is the likeliest possibility.

Sacrum

The sacral fragment (AMNH 259908) consists only of the first two sacral vertebrae (fig. 15). These vertebrae differ little from their equivalents in *Geocapromys,* and we cannot be certain that AMNH 259908 does not represent a hutia. However, it differs from all hutia sacra that we have examined in having a flat rather than highly contoured ventral alar surface, shorter and wider centra, and a broader dorsal alar surface. The size of the vertebral canal does not diminish greatly between S1 and S2, which may imply that the cauda equina was large and that therefore a tail of some sort was present. There are no other noteworthy features.

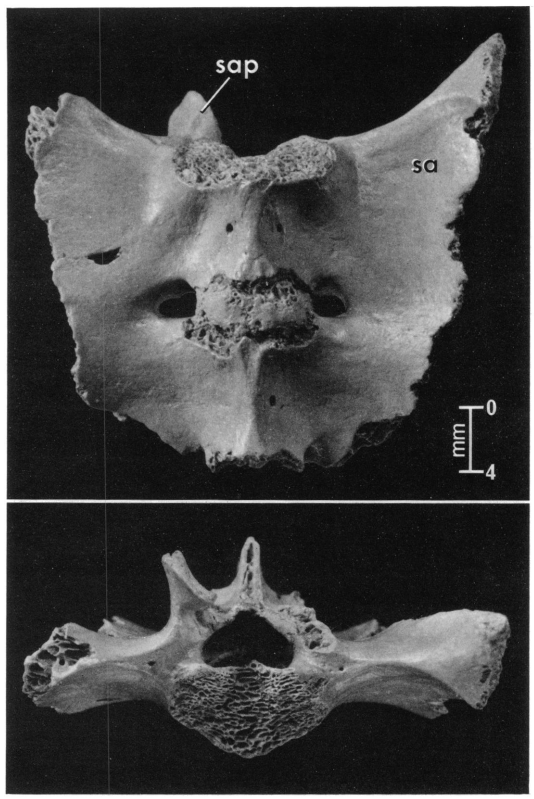


Fig. 15. Unattributed sacrum (AMNH 259908), Anthony Collection, Long Mile Cave. **Top.** Ventral. **Bottom.** Proximal.

DISCUSSION

Of the postcranial elements described in the preceding section, only the femur, os coxae, and tibiae are sufficiently like those of known Primates to warrant allocation to this order. Their provenance is the same as that of the *Xenothrix* holotype, which circumstantially supports the argument that all these specimens represent the same species and perhaps the same individual. We therefore place AMNH 259900, 259902, 259903, and 259904 in the hypodigm of *Xenothrix mcgregori.* The other bones described in this report are not systematically allocatable, at least not by us. This raises an important point. Until a few years ago, the land mammal species list for Jamaica was brief indeed: two extinct heptaxodontids, one extinct primate, one highly endangered cricetid, and a rarely seen capromyid (MacPhee et al., 1983). Now the list must be expanded to include the Coco Ree and Sheep Pen platyrrhines and the mammal, of unknown affinity, represented by the small humeri, the ulna, and possibly the sacrum from Long Mile. If, as we think probable, the large humerus represents yet another unnamed species, the Quaternary faunal list for Jamaica will have to be expanded to almost twice what it was only 5 years ago. This is of interest because Jamaica was previously thought to have been abnormally depauperate in mammals by comparison to the other Greater Antilles (MacPhee et al., 1983; Morgan and Woods, 1986). The Long Mile material is tantalizing evidence that we still have much to learn about the sub-Recent faunal composition of Jamaica.

This account would not be complete without considering the pertinence of historical records, for a very good reason. The mammalian fauna of the West Indies underwent

catastrophic reduction during the late Quaternary (MacPhee et al., 1989). If the majority of extinctions were induced anthropogenically, as many authorities have contended, they could not have occurred before the mid-Holocene (the consensus date for Amerindian colonization of the West Indies; Rouse and Allaire, 1978). Some occurred as late as the 16th century in Hispaniola (Anthony, 1918). Nothing is known about the timing of mammal losses in Jamaica (MacPhee et al., 1989), but it would be of interest to determine whether any species managed to survive into the early phases of European occupation of the island. In order to evaluate this possibility, we searched early historical records for allusions to unusual mammals. Nothing very useful was found, and here we shall limit discussion to the few reports that concern primates and animals described as "racoons."

PRIMATES: Several early natural histories of Jamaica mention primates, although in most cases it is specifically stated or can be inferred that the animals in question were imported. However, reports of monkeys that closely resemble species nowadays limited to South or Central America need to be carefully assessed. Denham (1987), for example, has discovered some unconfirmed historical evidence for the existence of an endemic cebid in Barbados, and debate continues as to whether the remains named *Ateles* [= *Montaneia*] *anthropomorphus* represent a native Cuban spider monkey (Arredondo and Varona, 1983) or an Amerindian import (MacPhee and Woods, 1982). There are no known records relating to the Cuban form; if a true endemic, it must have died out prior to the Spanish occupation.

Cave sites in western Cuba have recently yielded remains of another platyrrhine, *Paralouatta varonai* (Rivero and Arredondo, 1991). Although related to howler monkeys, *P. varonai* is clearly a distinct taxon. Long bones attributable to this species have been recovered and are currently undergoing study (MacPhee, in prep.). Here it is sufficient to note that *Paralouatta* and *Xenothrix* do not display any important postcranial resemblances that would justify the hypothesis that they are closely related.

Importation of exotic mammals seems to have been a thriving enterprise in 18th-century Jamaica, which by then had become wealthy from sugar. In addition to the usual run of domesticated mammals, Browne (1789) mentioned the introduction of camels, sloths, squirrels, rabbits, otters, possums, bears, and mongooses, as well as several kinds of monkeys. One especially unusual introduction, mentioned in Sloane's (1707–25) remarkably comprehensive study of the natural history of Jamaica, deserves brief notice:

> *Cercopithecus Indicus Bugee dictus . . . Simia-sciureus lanuginosus fuscus ex Joannae insula*[.] *Petiver. Gaz. Nat. Tab. 17. Fig. 5. A Bugee from Joanna.*
>
> These are frequently brought hither by Ships from the Island of *Joanna,* and other Parts (Sloane, 1725: 329).

The nomen *Cercopithecus* was indiscriminately applied to various primate taxa until the late 18th century (cf. Hershkovitz, 1977), and we cannot assume that Sloane meant to refer to a catarrhine monkey. Indeed, Sloane's text indicates that he believed that the Jamaican animals were closest to the "*Cercopithecus*" from the island of Joanna as illustrated by James Petiver in 1703 (see Tattersall [1982] and fig. 16). This was an unusual comparison on his part, because Petiver's "bugee" from Joanna (i.e., Anjouan in the Comores Archipelago) is clearly a lemur, probably *Lemur mongoz* (Tattersall, 1982). If Sloane meant to refer to a lemur—and there is no way of confirming this—this passage may stand as the earliest known record of the importation of a nonanthropoid primate into the New World.

RACOONS: In addition to bugees, Sloane (1725: 329) also mentioned the existence of a mammal which he called a "racoon":

> *Vulpi affinis Americana; Coati Boasiliensibus* [?Brasiliensibus] *Marcgr. Rattoon seu Rackoon. . . .*
>
> The Racoons are commonly here in the Mountains, and live in hollow fiddlewood Trees, from whence they make Paths to go to seek Sugar Canes, which is their chief, if not only Sustenance.

Goldman (1950) and other procyonid specialists have dismissed Sloane's "racoon" as either an introduction or a fantasy, although it may be noted that species of *Procyon* apparently distinct from continental *P. lotor* recently existed on several small islands in the Caribbean Sea (Goldman, 1950; Hall, 1981).

Fig. 16. Plate 17 from Petiver's *Gazophylacii Naturae,* probably published about 1703 (see Tattersall, 1982). Figure 5 is identified in an accompanying index as a "Bugee from Joanna," and may have been based on a specimen of *Lemur mongoz* from Anjouan in the Comores. The other animals and plants in this plate are identified as North American, African, or Asian; none is Malagasy or Comorian.

These racoons are the only mammalian carnivores known to have penetrated the West Indies without evident human assistance. (*Cubacyon transversidens* [Arrendondo and Varona, 1974] is more likely to be an Amerindian dog than a native canid.) The "silent dogs" of Hispaniola mentioned by early Spanish explorers (e.g., Oviedo; cf. Stroudmire, 1959) have been interpreted as true racoons, but there is no reliable evidence that *Procyon* managed to invade any of the Greater Antilles (cf. Allen, 1911; Hershkovitz, 1966; Arredondo, 1976).

There are two other possible explanations for Sloane's "racoon." The first and more conservative is that Sloane's "racoon" is actually the hutia, *Geocapromys.* The basis for this interpretation is a passage in Browne's (1789) work. Under his listing for *Mus,* Browne (1789: 484) mentioned an animal which was locally known as the "Spanish Racoon." This "racoon" was described as having been imported into Jamaica "from *Cuba* and the neighbouring islands, where it is most common: its eyes, lips and teeth, are like those of a rabbit, but the ears are shorter and smaller, though much of the same form." He went on to compare it to the "small *Indian* Coney," which it resembled closely except for its longer tail. The small coney, described by Browne as a native to Jamaica, is without doubt *Geocapromys*; the "Spanish Racoon" seems almost certain to be its close relative *Capromys,* which (among other features) is distinguished by its greater tail length (Anderson et al., 1983). This suggests that, in 18th-century Jamaica, "racoon" and "coney" were used interchangeably as common names for capromyids. This helps to explain the otherwise inexplicable omission of any reference to hutias per se in Sloane's (1725) mammal list—an omission that does not appear to have been previously noticed (cf. Allen, 1911). The only difficulty with this reasoning is that Sloane was an extremely acute observer, and it is peculiar that he would have

mixed up a rodent with a carnivore—especially since he added a footnote to his description of the Jamaican "racoon" which explicitly associates it with the "Racoon of Josselyn" (a reference to a late 17th-century observation of *Procyon lotor* in New England).

The second interpretation is that Jamaica supported a native procyonid. Other than Sloane's text, the only original documentary evidence for this argument consists of some brief remarks by Pennant (1771) and Buffon (1776) concerning an unusual mammal allegedly found in the "mountains of Jamaica." Although these authors' accounts differ in minor details, it is reasonably clear that their observations pertain to a single animal, kept by a certain Mr. Colinson in the late 1760s (Pennant, 1771: 134; Buffon, 1776: 252, footnote g). Pennant's (1771) detailed trait list suggests that he must have examined this animal personally, probably when it was put on exhibit in London in 1769 by its "keeper" (presumably Colinson, although no name is mentioned). Buffon's (1776) description is based solely on a letter and drawing which Colinson sent to him in December, 1766. The publication of Buffon's (1776) description postdates Pennant's (1771), but there is no textual evidence that he consulted Pennant's account.

Buffon's and Pennant's systematic conclusions regarding Colinson's animal were quite different. Buffon (1776: 252) claimed, presumably on Colinson's authority, that the indigenous name for the animal was "poto." Pennant (1771: 139) said much the same thing, noting that it was known by the name "*Potto,* the name given by some writers to a species of *Sloth,* found in *Guinea.*" However, Buffon decided that the specimen most closely resembled the kinkajou of New Spain, then poorly known in Europe, and compared the two in plates (fig. 17). Pennant (1771) did not make this comparison, and it is probable that kinkajous were not then known to him. In his view, Colinson's animal belonged with the lorises and lemurs (defined by Pennant as mammals with six cutting teeth, foxlike faces, and feet formed like hands). Additionally impressed by the tail, which had "the same prehensile faculty as some of the monkies have" (p. 139), Pennant gave the animal a name which reflected its apparent relationship to primates—"Yellow Maucauco" (fig. 18). In this he was followed by Schreber (1774: 145), who formally included Pennant's yellow maucauco in *Lemur* as *L. flavus.*[3] These allocations were soon challenged by other naturalists, and both authors later transferred the Jamaican species from primates to carnivores (renaming it as the "Yellow Weesel" in Pennant's [1781] case and *Viverra caudivolvula* in Schreber's [1778: 453]). However, it was not until the early part of the 19th century that consensus was reached that this animal must have been a kinkajou, and that kinkajous were definitely related to procyonids and not primates (e.g., Cuvier, 1822; Owen, 1835). Since that time, no additional examples of kinkajous have come from Jamaica, although Gosse (1851) mentioned the existence of a rarely seen carnivore locally known as the "Charley Price Rat." This animal was too vaguely described for Gosse to identify, and he accepted the explanation that it was an introduced species. Other authors who have traced parts of this story have concluded that the Jamaican record is spurious, and that Colinson's animal probably came from northern South America (Thomas, 1902; Hussan, 1978; Ford and Hoffmann, 1988).

[3] Kortlucke (1973: 3–4) pointed out that the animal depicted by Schreber (1774) in his plate 42—designated as an illustration of his *Lemur flavus*—is not based on Pennant's (1771) drawing of a "Yellow Maucauco," but instead illustrates "an unidentifiable composite animal whose characters do not correspond with the written description." The animal in question is clearly a copy of Petiver's bugee from Joanna (Hussan, 1978). Kortlucke (1973) failed to note that Schreber (1778: 453), apparently irritated by the fact that he was earlier drawn into believing that kinkajous were lemurs on the basis of Pennant's drawing, decided to suppress his original plate 42 and to substitute a new illustration (plate 125B) from Vosmaer. The copy of Petiver's bugee was not part of the original series of plates for the first part of his work, but was separately published (with several other supplemental plates) in 1778 together with the plates for the third part (cf. Schreber, 1778: 590; Wagner, 1846: 427; but for other interpretations and chronologies see Hussan, 1978: 289). Why he chose to give it the same number as the suppressed Pennant copy is not clear; it must have been accidental, however, because even in 1774 Schreber (cf. p. 137) clearly distinguished *Lemur simia-sciurus* from *L. flavus.*

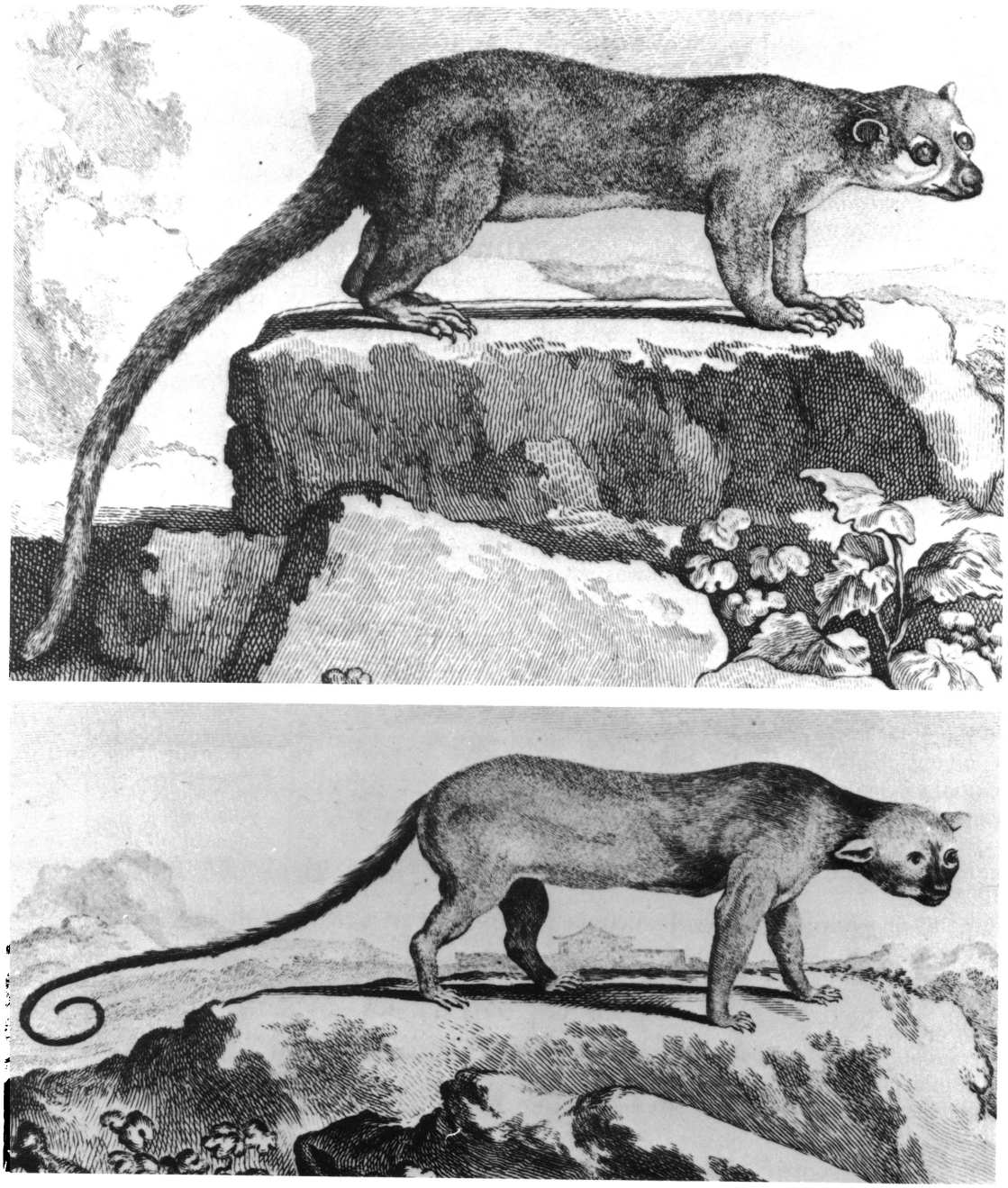


Fig. 17. "Le Kinkajou" (**top**) and "Le Potot ou Kinkajou Potot" (**bottom**) of Buffon (1776: plates 24 and 25). The kinkajou is presumably based on a specimen from New Spain; the kinkajou potot, on Colinson's drawing of the "poto" from the "mountains of Jamaica."

The last element requiring clarification in this confusing story is the name "poto" or "potto." "Potto" is based on a Guinean word for the lorisine *Perodicticus* (Palmer, 1904). Cuvier (1822) suggested that "poto," as applied to the kinkajou, was a simple case of transference, probably on the part of African slaves who used this name to describe a crea-

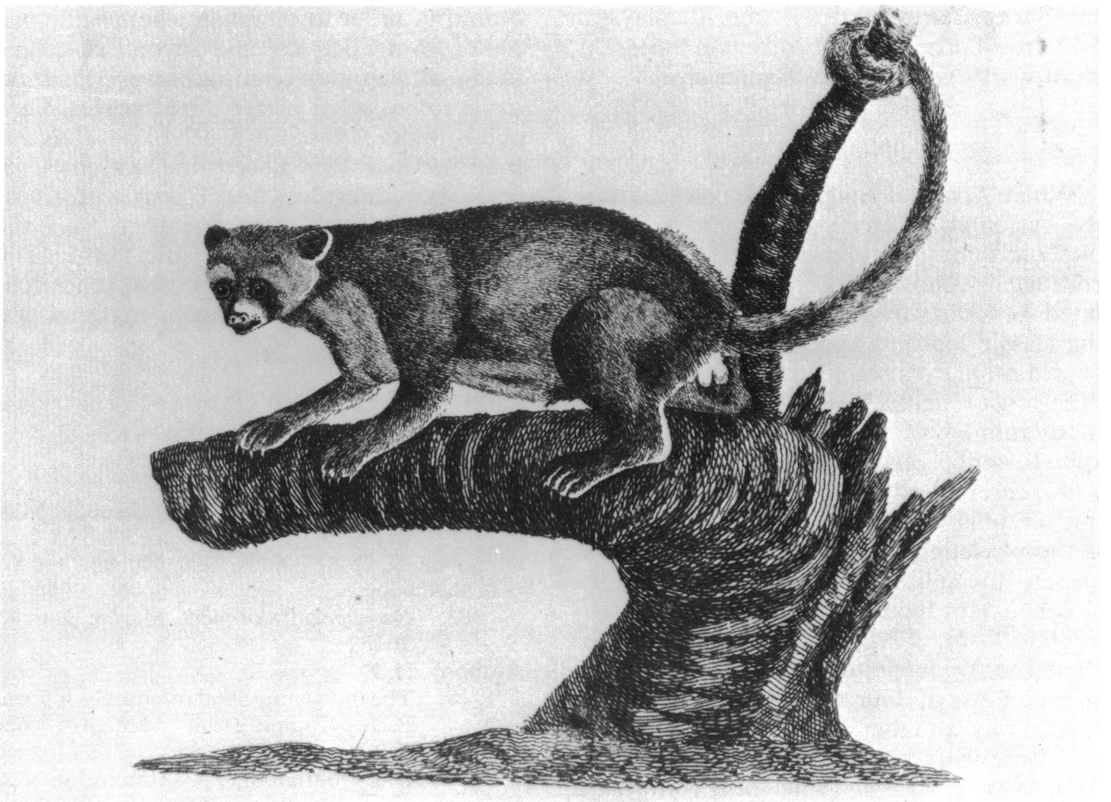


Fig. 18. "Yellow Maucauco" of Pennant, originally classified as a lemur (Pennant, 1771) and later as a carnivore (Pennant, 1781). Apparently based on a living specimen exhibited in London in 1769 (Colinson's specimen?). This plate, from Pennant's (1781: plate 36) second book, is identical to the one published in his first.

ture which they thought resembled some lorisoid from their homeland. If so, it is easy to see the basis for their confusion: with its large ears, comparatively short face, woolly pelt, and large, frontated orbits, *Potos* is externally somewhat like a large *Galago* or *Mirza*. Indeed, one of the current common names for *Potos* is "night-ape." Sanderson (1949: 771) noted that local people in countries where kinkajous are common "cannot be shaken in their belief that this animal is a monkey."

Interestingly, the similarity to certain primates does not end with external anatomy. The mandible of *Potos* exhibits a deep ramus, flared gonial region, fused mental symphysis, two low and mesiodistally elongated molars, and three premolars whose roots decrease in size from front to back. Some of these features are seen in callitrichids; all of them are found in *Xenothrix*. In fact, what clearly distinguishes the jaw of *Xenothrix* from that of *Potos* is not molar morphology per se but the character of the anterior dentition—about which we know nothing other than root size in the case of the Jamaican primate. Yet in having only four incisors, *Xenothrix* differs from all Recent Carnivora except *Enhydra*, and its apparently tiny canines have no parallel among other members of this order (ignoring taxa whose entire dentitions are reduced, such as *Eupleres*).

In the absence of any dispositive information, further speculation about the identity of Colinson's "poto" is pointless. Although we continue to favor the opinion that *Xenothrix* is a platyrrhine, we wonder whether it could have been enough like a racoon or kinkajou in its external morphology to serve as a basis for some of the anecdotes referenced above. This point also applies to

the Sheep Pen primate; it, too, displays an odd mix of primate and carnivoran traits (e.g., shaft width vs. lesser trochanter size).

CONCLUSION

Where *Xenothrix* ought to be placed within the systematic framework of Platyrrhini is likely to remain a vexing issue. The fact that competent taxonomists have successively rotated *Xenothrix* into—and out of—several of the classic families and subfamilies of New World monkeys establishes its credentials as "the most enigmatic of all South American fossil monkeys" (Simons, 1972: 184). Despite Rosenberger's (1981; Rosenberger et al., 1990) careful and detailed analyses, it is still not obvious which major platyrrhine group is the phyletic sister of *Xenothrix,* nor how ancient the split between this taxon and its closest extant relatives might be (see, in particular, Ford, 1990). The postcranials assigned to *Xenothrix* in this paper do not resemble those of douroucoulis and titis in any special way, and therefore provide no support for Rosenberger's (1977) hypothesis that *Xenothrix, Callicebus,* and *Aotus* comprise a separate monophyletic group within Platyrrhini. In our view, *Xenothrix* appears to have been at least as morphologically distinct from Cebidae, Atelidae, and Callitrichidae as representative members of these families are from one another. This suggests that the appropriate course is to embrace Hershkovitz' (1970) proposal to place *Xenothrix* in a separate family, Xenotrichidae. Such a procedure may be messy taxonomically, but in the absence of demonstrable synapomorphies linking *Xenothrix* to any single monophyletic group within Platyrrhini, it is justified. Like Xenotrichidae, some other Antillean families (e.g., Solenodontidae, Heptaxodontidae) are hard to place within their respective suborders and superfamilies, for the same reason: substantial morphological divergence from their continental relatives, occasioned by long isolation (cf. MacFadden, 1980; Patterson and Wood, 1982). Leaving these families as incertae sedis within their respective major taxa should be seen as an inducement to further research, not as a threat to tidy systematic housekeeping.

Specimens other than femora will be required in order to establish whether the primates from Coco Ree and Sheep Pen belong in the same monophyletic group as *Xenothrix* or represent other platyrrhine lineages. Ford and Morgan (1986; Ford, 1990) have argued that the Coco Ree platyrrhine exhibits femoral synapomorphies that link it with Callitrichidae, but they were unable to place the Sheep Pen species in any existing family. The latter may or may not be a second xenotrichid; only the evidence of better material will tell.

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Sulawesi Rodents (Muridae: Murinae): Morphological and Geographical Boundaries of Species in the *Rattus hoffmanni* Group and a New Species from Pulau Peleng

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ABSTRACT

Characters derived from museum skins, skulls, dentitions, karyotypes (for *R. hoffmanni*), and ecologies allow the descriptions and definitions of native *Rattus* occurring in the Sulawesi region. *Rattus hoffmanni,* which is primarily terrestrial and frugivorous, inhabits most forest formations at nearly all altitudes throughout mainland Sulawesi and on some small islands nearby. *Rattus mollicomulus,* a smaller-bodied relative of *R. hoffmanni,* is found only on the higher slopes of Gunung Lompobatang near the tip of the southwestern peninsula of the island. *Rattus koopmani,* new species, is one of the few native murids recorded from Pulau Peleng in Kepulauan Banggai off the east coast of central Sulawesi. Morphological and distributional features of the three species are compared with non-native species of *Rattus* (*R. rattus, R. nitidus, R. exulans, R. argentiventer,* and *R. norvegicus*) and with species indigenous to islands east and west of Sulawesi (*R. tawitawiensis* from the Sulu islands, *R. elaphinus* from Pulau Taliabu in Kepulauan Sula, and *R. feliceus* from Pulau Seram in the Malukus). The generic allocation of species in the *R. hoffmanni* Group (*hoffmanni* and *mollicomulus*) is discussed, as are faunal associations of the three Sulawesi species with the rest of the native Sulawesian murids. Definition of species and distributional boundaries is the first part of a broader inquiry into phylogenetic relationships between *R. hoffmanni* and the other species of *Rattus* in the Indo-Australian region.

INTRODUCTION

The night wind sighs, the clouds part, and the moon falls through the dark crowns, splashing over forest floor and tree trunk. Moonlight replaces yellow glow of dusk, but the warm breath of tropical forest lingers to nourish the canopy-formers latticed together by ropy vines and leafy understory. The interplay of pale light and shadow dapples stretching buttresses of great trees and choking roots of emergent strangler figs. Soft calls from a distant owl counterpoint the rustle of leaf litter as a small animal scurries from beneath rattan rosettes and bushy tangles for the inky darkness alongside the mossy trunk of a fallen giant. Invisible in the shadows, the animal darts across the clearing and takes on form and motion in the muted spotlight from between the clouds. A glimpse of dark fur and long tail is the fleeting record left behind as it disappears beneath the trunk. Palm leaflets clatter against each other, signalling a renewed wind that bends the leafy branches of understory trees, rustles the more resistant crowns of the canopy, and finally closes the stormy clouds to seal the forest from the moonlit vault of sky.

The animal is *Rattus hoffmanni.* The place is Sulawesi, the first large island east of Bor-

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Fig. 1. Tropical lowland evergreen rain forest at 30 m, near Kuala Navusu, 1975. The palm in the foreground is *Licuala celebica,* endemic to Sulawesi (Dransfield, 1981). Another Sulawesian endemic, *Rattus hoffmanni,* lives in these kinds of lowland tropical forest formations, where ambient air temperatures are moderately high (table 4), the canopy trees tall, and the forest rich in species of trees, palms, woody vines, understory plants, and other kinds of vegetation (Musser and Dagosto, 1987).

neo. The time is flexible: it is now, it stretches back into the evolutionary beginnings of forest and rat, it will extend into the future as long as present flora and fauna coexist without significant alteration.

Rattus hoffmanni is a chunky animal with a long head, large eyes and ears, brown fur, and a moderately long brown tail. It lives in primary forest (fig. 1) and is found in tropical formations from near sea level to mountain summit. It is nocturnal, primarily terrestrial, and eats fruit pulp and seeds. The species is found on Sulawesi and some small islands off the coast, but nowhere else. It has a relative living in mountain forest on the slopes of an old volcano at the end of the southwestern arm of Sulawesi. It may also be related to a large-bodied rat that is known only from Pulau Peleng in the Banggai Archipelago off the eastern coast of central Sulawesi.

The morphological and geographical boundaries of *R. hoffmanni,* its relative in the southwest, and the Peleng animal are important to define because more than half of the endemic mammalian fauna peculiar to Sulawesi consists of murid rodents (Musser, 1987). Illuminating the species boundaries of *R. hoffmanni* and its relatives will add to our understanding of this insular evolutionary diversity, which is reflected in an impressive range of morphologies and life styles. Furthermore, these definitions will help clarify the contents of the genus *Rattus* as well as its diagnostic characters and geographic range. Our focus on Sulawesi *Rattus* and our search for species limits are presented in a particular context involving a more general *Rattus* problem and an operational species definition, a context that we now explain.

The *Rattus* Problem

In his monumental compilation of the families and genera of rodents, Ellerman (1941, 1949) recognized more than 540 forms of *Rattus,* making the genus unequaled among living rodents in the spectrum of morphological diversity it delimited and the number of species and subspecies it contained. To Ellerman, Europe, Africa, and Asia were the evolutionary homelands of the genus, but the greatest species and morphological diversity was to be found in the Indo-Malayan and Indo-Australian regions. On islands and the peninsula of the Sunda Shelf, for example, about 60 percent (23 of 38 species) of the native rats and mice were thought to represent species of *Rattus* (Chasen, 1940; Ellerman, 1941; Musser and Newcomb, 1983: 528). But it was the large island of Sulawesi to the east of the continental margin defining the Shelf that held the most expansive evolutionary radiation of forms of *Rattus.* For its area, not only did Sulawesi contain the largest native fauna of murid rodents, but 81–87 percent of the indigenous murids were identified as *Rattus* (table 1) in early reports (Raven, 1935, for example) and up into the 1970s (Groves, 1976). So impressive was this representation that some speculated Sulawesi to have been the center of origin and dispersal of the genus (Groves, 1976).

That perception has changed. During the last decade, taxonomic inquiries concerning the Indo-Malayan and Indo-Australian faunas have focused on defining the morphological and distributional limits of murid species as an initial phase in uncovering patterns of phylogenetic relationships and then inferring evolutionary histories in time and space. As a result, the content of *Rattus* has diminished. Studies have shown that the morphologies of certain species either fitted the range of variation seen in other genera or constituted new generic clusters not closely related to *Rattus.* By the early 1980s, interpretation of relationships among rats and mice native to the Sunda Shelf had shifted dramatically from the earlier impression that species of *Rattus* are the dominant component of the fauna to the current perception that they are a minor element (Musser and Newcomb, 1983). The most recent survey reveals that of the 41 native species, only 5 remain in *Rattus*—a change from 60 to 12 percent of the murid fauna—and that even some of those 5 may eventually be extracted from the genus (Musser, 1986).

The view of *Rattus* on Sulawesi has been similarly transformed. The idea that species of the genus constitute more than 80 percent of the native murids has been altered by the realization that they form only a small part of the indigenous assemblage, about 19 percent (table 1): two species in the *R. hoffmanni* group (*hoffmanni* and *mollicomulus*), a new

species from Pulau Peleng, and six species in the *R. xanthurus* group (*xanthurus, marmosurus, facetus, bontanus, foramineus,* and *pelurus*) (table 17). The *xanthurus* group retains many primitive morphological characters as well as derived features untypical of *Rattus* and may prove to be part of a monophyletic cluster outside of the one formed by species of that genus (Musser and Holden, in prep.). Therefore, the members of the *R. hoffmanni* group and the Peleng rat may be the only living indigenous representatives of the genus *Rattus* on Sulawesi and nearby islands.

These studies of the Indo-Australian rodent faunas have not only pinpointed the native *Rattus* but have also identified those species occurring on a particular island or in a certain archipelago that are not endemic, whose presence reflects dispersal mediated by human activity. In addition to the endemic *Rattus* on Sulawesi, for example, five other species are found there (*R. rattus, R. nitidus, R. argentiventer, R. exulans,* and *R. norvegicus*), but not one of them is indigenous to the island (Musser, 1977, 1987). One result of the inquiry into phylogenetic relationships of the native murids in general and the endemic species of *Rattus* in particular has been the recognition of these species as non-native, introduced components of the Sulawesian fauna.

Refining the morphological, distributional, and ecological characteristics of true native *Rattus* on Sulawesi will allow the formulation of questions related to their relationships with the rest of the Sulawesian murids. It also will allow comparison with the species of *Rattus* indigenous to mainland Southeast Asia, islands and the peninsula of the Sunda Shelf, and islands ringing the continental margin to the west of Sulawesi, on one hand; and with those species native to the Moluccas, New Guinea, Australia, and the Nusa Tenggara, to the east, on the other. Although the species of *Rattus* may represent a minor part of the diversity in faunas native to Southeast Asia and Sulawesi, they are still considered by some workers to constitute a significant portion of the rodent groups peculiar to New Guinea (Taylor et al., 1982) and Australia (Taylor and Horner, 1973), and a minor component of the fauna on Timor (Kitchener et al., in press) and on Flores (Kitchener et al., in press).

TABLE 1

The Number of Indigenous Sulawesian Species in *Rattus* and in Genera Other than *Rattus* Recognized by Various Authors between 1935 and 1991[a]

Author	*Rattus*	Other genera	Total
Raven (1935)	29 (81%)	7 (19%)	36
Tate (1936)	32 (87%)	5 (13%)	37
Laurie and Hill (1954)	30 (86%)	5 (14%)	35
Corbet and Hill (1980)	22 (69%)	10 (31%)	32
Musser (1984)	4 (10%)	31 (90%)	35
Present report (table 17)	9 (19%)	39 (81%)	48

[a] We begin with Raven's treatise on *Wallace's Line and the Distribution of Indo-Australian Mammals* because it lists species described before 1935 as well as all the new Sulawesian taxa proposed by Miller and Hollister in 1921 (a and b), contributions that significantly increased knowledge of diversity at specific and generic levels over what was known prior to 1921. Laurie and Hill's *List of Land Mammals of New Guinea, Celebes and Adjacent Islands, 1758 to 1952* includes the arrangements in checklists and faunal studies relating to the Sulawesian fauna after 1936, such as those by Ellerman (1941, 1949). Data in table 17 are extracted from Musser (1981a, 1982b, 1991), from Musser and Newcomb (1983), from publications cited in Musser (1984), and from manuscripts being prepared for publication. Our figures also include the species and their generic allocations listed by Corbet and Hill (1986), who referred to the publications by Musser and his colleagues for Sulawesian entries in the second edition of their *World List of Mammalian Species.*

Where do the Sulawesian species of *Rattus* fit within the phylogenetic relationships among all the species native to that broad geographic swath from mainland Asia through the Moluccas and Nusa Tenggara to the New Guinea and Australian region? There is a published hypothesis that "Sulawesi is a large oceanic island supporting a native and endemic mammal fauna that, with the exception of phalangers, had its origin on mainland Asia" (Musser, 1987: 90). Does this really apply to *Rattus hoffmanni* and its relative, to the Peleng species, and possibly to members of the *R. xanthurus* group?

Another suggestion has been made in the context of asking what species of *Rattus* "may have been on the Sunda Shelf in the past when Sundaland consisted of islands and peninsula during times of high sea levels and

a large continental expanse above water at times of lower sea levels" (Musser and Heaney, 1985: 30). Possibly an "ancestral species occurred there that is absent from the Recent fauna and now represented by *R. stoicus* in the Andaman islands, *R. palmarum* and *R. burrus* in the Nicobars, *R. simalurensis* in the Simalur Islands, *R. lugens* in the Mentawais, *R. adustus* on Pulau Enggano, *R. hoffmanni* on Sulawesi, and *R. tawitawiensis* in the Sula Archipelago" (Musser and Heaney, 1985: 30). Are members of the *R. hoffmanni* group more closely related to these insular species than to the native *Rattus* found on the Sunda Shelf and mainland Asia?

Is the West the wrong direction to look toward for answers to questions about relationships of the Sulawesi species of *Rattus*? Should answers be sought from the East? If the morphologies of some or all of the species endemic to Australia, New Guinea, the Moluccas, and the Lesser Sundas are really contained within the limits of *Rattus,* Sulawesi occupies a pivotal geographic position between western and eastern faunas. Characteristics of the *Rattus* found on that island may or may not provide clues to the phylogenetic relationships and geographic origins (whether dispersal or vicariant events) responsible for the scatter of *Rattus* species from Asia to the New Guinea and Australian regions (Musser, 1981b).

Identification of the species of true *Rattus* native to Sulawesi and documentation of their characteristics become important within the context defined by these avenues of inquiry. That is why we focus on some Sulawesian *Rattus* in this report and why paragraphs are devoted to morphological descriptions of the species, to comparisons between each of them and other kinds of *Rattus,* and to the outlines of geographic ranges and altitudinal distributions. Accordingly, we here document the nature of members of the *R. hoffmanni* group and of the new species from Pulau Peleng. Analyses of the *R. xanthurus* group will be provided at a later time (Musser and Holden, in prep.).

Species Limits

We use the morphological and geographical distributions of samples described here to estimate species boundaries. All but two allopatric populations occur on different islands. Two distinct morphological groups exist on the southwestern peninsula of Sulawesi, but evidence from present samples suggests even these to be altitudinally allopatric in distribution. We consider populations which exhibit distinct morphologies that are diagnosable regardless of geographical distribution to be independent lineages. We realize that morphological change and geographic isolation do not necessarily coincide with speciation. However, the species limits proposed by us are hypotheses that may be supported or rejected with acquisition and analyses of additional information.

Abbreviations and Methods

Institutions and Specimens: Results of our report are based on personal examination of specimens stored in collections of the American Museum of Natural History, New York (AMNH); the Philadelphia Academy of Natural Sciences, Philadelphia (ANSP); the British Museum (Natural History), London (BM); the Field Museum of Natural History, Chicago (FMNH); the Museum of Comparative Zoology at Harvard University, Cambridge (MCZ); the Museum Zoologicum Bogoriense, Bogor (MZB); the Staatliches Museum für Tierkunde, Dresden (SMT); the South Australian Museum, Adelaide (SAM); the Rijksmusem van Natuurlijke Historie, Leiden (RMNH); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and the Zoological Museum of the University of Amsterdam (ZMA). Museum catalog numbers of specimens referred to in the text are preceded by one of these acronyms.

Most characters we discuss are those found in a stuffed skin—the standard museum preparation—with an associated cranium and mandible. Color notations of the ears, feet, and tail of *Rattus hoffmanni* were supplemented by information from Musser's field catalogs, where chromatic descriptions of live animals trapped in central Sulawesi are recorded. We also relied on material stored in 70 percent ethanol (originally preserved in a formalin solution) for our description of pal-

mar and plantar surface topography. We recognize that the morphological bias of the data permits only incomplete descriptions of species in the *R. hoffmanni* group and of the new species from Pulau Peleng, but the available study material necessitates this bias. The Pulau Peleng animal is known only by a skin and skull, and most of the distributional picture of *R. hoffmanni* and its ally is dependent upon conventional museum preparations. There are adequate series of *R. hoffmanni* from central Sulawesi that are preserved in fluid, and these will be used to investigate characters of other anatomical systems in a study designed to seek possible phylogenetic relationships between *R. hoffmanni* and all of the other murid rodents endemic to Sulawesi (Musser, in prep.).

MEASUREMENTS: Values for total length, length of tail (LT), and length of ear (LE) are those recorded by collectors on labels attached to skins; subtracting length of tail from total length gave us length of head and body (LHB). The number of scale rings per centimeter (TSR/cm) was counted on the tail about a third the distance from its base. Values for length of hind foot, including the claw (LHF), were either taken from skin labels (collections made by Musser during the Archbold Sulawesi Expedition) or from our measurements of dry study skins (all other museum specimens). Of these four external dimensions, length of hind foot is the only reliable measurement for most collections. Lengths of head and body as well as tail, for example, were taken by different collectors and some of the individual and geographic variation shown by these measurements is due to different measuring techniques. Where we have been able to test results of different collectors, we found the values given by Sody (specimens in RMNH), Raven (series in USNM), and Frost (material in BM) to be the most reliable. Those obtained by other collectors, particularly either Heinrich or Menden (collections in AMNH), proved to be inaccurate. Menden apparently included the base of the tail within his measurement of head and body, and Heinrich's figures for tail length are exaggerated because of his tendency to incorporate part of the rump.

Using dial calipers graduated to tenths of millimeters, we took the following cranial and dental measurements (listed in the sequence in which they appear in the tables):

GLS	greatest length of skull
ZY	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
DZN	depth of zygomatic notch
LD	length of diastema
PPL	postpalatal length
LBP	length of bony palate (palatal bridge)
BBPM1	breadth of bony palate at first molar
BBPM3	breadth of bony palate at third molar
EBPM3	extension of bony palate posterior to back margins of third molars
LIF	length of incisive foramina
BIF	breadth of incisive foramina
BMF	breadth of mesopterygoid fossa
LB	length of auditory bulla
CLM1–3	crown length of maxillary molar row
clm1–3	crown length of mandibular molar row
alm1–3	alveolar length of mandibular molar row
BM1	breadth of first upper molar
bm1, bm2, bm3	breadths of first, second, and third lower molars

The measurements are defined in Musser and Newcomb (1983) and Musser (1984), and their limits are illustrated in figure 2; values are given in millimeters.

DENTAL TERMINOLOGY: The names we use for cusps and cusplets of upper and lower molars are presented in figure 3.

CHROMOSOMES: Karyotypes of *R. hoffmanni* are described. They were prepared and stained in the field from chromosomes of bone marrow, and processed by employing colchicine, hypotonic citrate, and flame-drying procedures outlined by Patton (1967).

We employ four terms to describe the shape of each chromosome relative to position of the centromere: **metacentric** (the chromosome is biarmed, one arm being about the same length as the other); **submetacentric** (one arm is shorter than the other, about a third of its length); **subtelocentric** (one arm is very short relative to the long arm on the other side of the centromere); and **telocentric** (the centromere is at the tip of the chromosome or near enough that any portion on the other

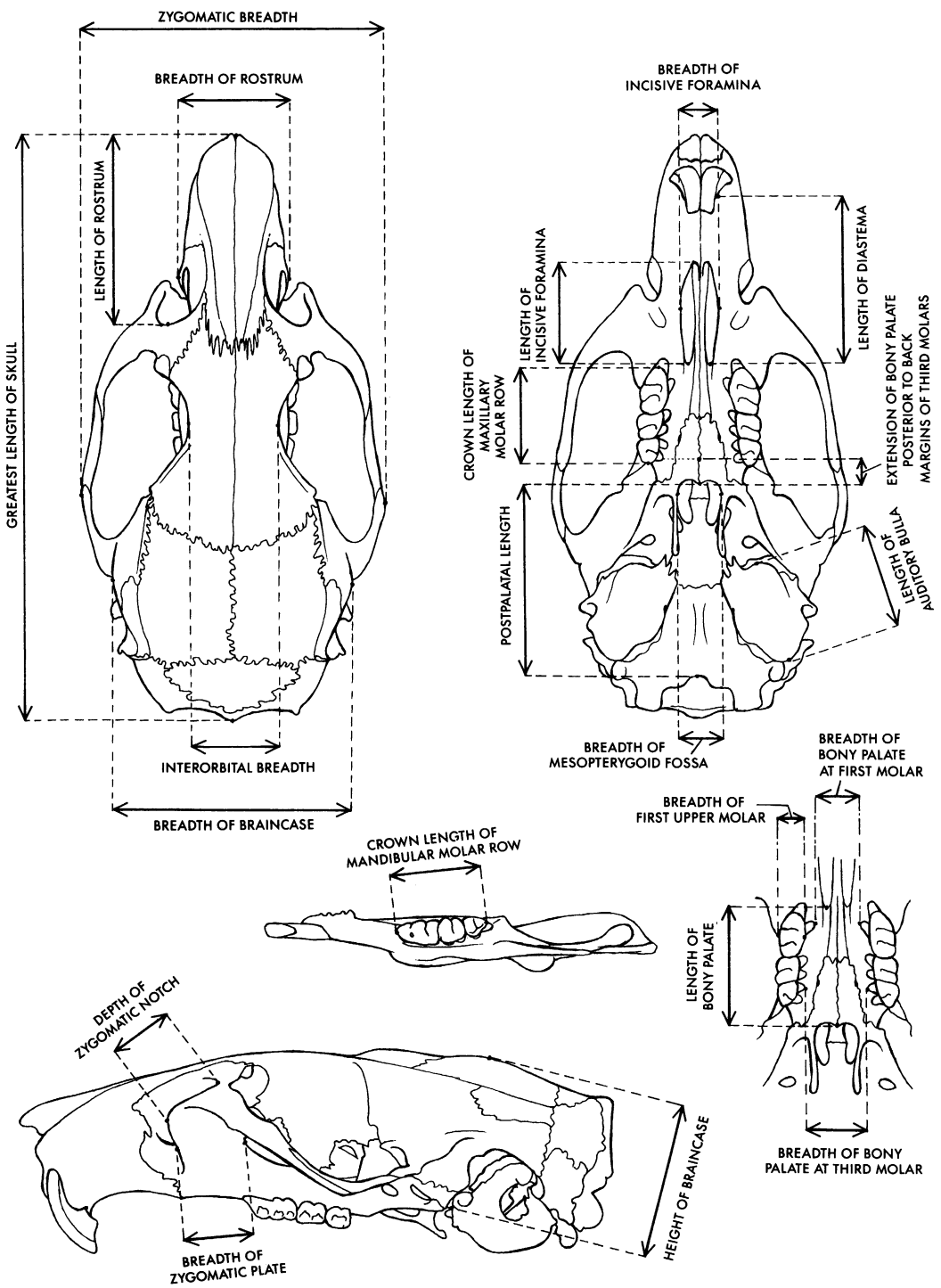


Fig. 2. Views of cranium and molars of an adult *Rattus hoffmanni* showing limits of cranial and dental measurements.

side of the centromere is so short as to be indistinguishable or nearly so).

RATIO DIAGRAMS: Proportional relationships among species are illustrated by ratio diagrams (figs. 31, 34). Simpson (1941) described the method for these kinds of charts but ours require additional explanation. For each measurement, the absolute value of the mean and plus and minus two standard errors of the mean were converted to logarithms. For each dimension, the logarithm of the mean of the standard (*Rattus hoffmanni* in each diagram) was subtracted from the logarithm of the mean of each sample to be compared with the standard, and the logarithms of plus and minus two standard errors of the mean of the standard were subtracted from the logarithms of plus and minus two standard errors of the mean of each comparative sample. Measurements larger than the standard are represented on the diagram by positive values, those smaller by negative values. In each sample, the solid or dashed lines connect the means of measurements, the horizontal bars or broken lines represent plus and minus two standard errors of the mean. A sample with the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the samples being compared with the standard are similar in absolute size they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar.

STATISTICS: We employed descriptive statistics to calculate the mean, standard deviation, and observed range for each measurement. We tested the significance of the difference between two sample means by a *t*-test. Wherever in the text we refer to the differences between sample means as being significant, we are rejecting the null hypothesis using the 0.05 level of significance. Probability values resulting from comparisons among all the samples of *R. hoffmanni,* and between those samples and the series of *R. elaphinus,* are on file in the Department of Mammalogy at the American Museum of Natural History.

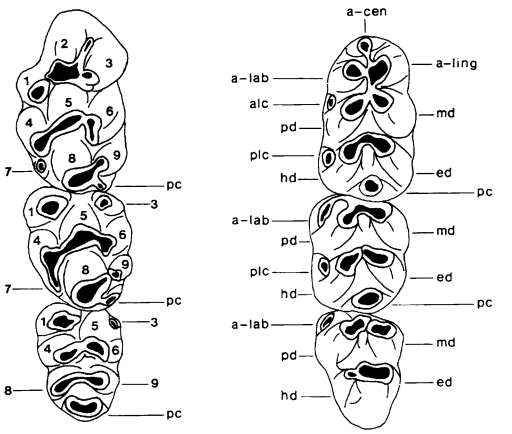


Fig. 3. Diagram of upper **(left)** and lower **(right)** molars of *Lenothrix canus* illustrating structural terms. Upper molars: cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix t; **pc,** posterior cingulum. Lower molars: **a-cen,** anterocentral cusp; **a-lab,** anterolabial cusp; **a-ling,** anterolingual cusp; **pd,** protoconid; **hd,** hypoconid; **md,** metaconid; **ed,** entoconid; **pc,** posterior cingulum; **alc,** anterior labial cusplet; **plc,** posterior labial cusplet.

GEOGRAPHY: A generalized reference map of Sulawesi and nearby islands is provided in figure 4. Many of the place names and their coordinates that are listed in the gazetteer of primary collecting localities were taken from *Gazetteer of Indonesia, Third Edition* (names approved by the United States Board on Geographic Names, published by the Defense Mapping Agency, September 1982). Spellings of several other place names are from Musser's field notes and coordinates for these as well as some other places were estimated from Joint Operations Graphic-Ground Topographic Maps, scale 1:250,000 (compiled by Mapping and Charting Establishment RE, 1969, and published by the Director of Military Survey, Ministry of Defence, United Kingdom, 1970).

Throughout the report we use the Indonesian terms *sungai* (stream or small river), *kuala* (stream discharging directly into the sea), *gunung* (mountain), *pegunungan* (mountain range), *pulau* (island), *kepulauan* (archipelago), *selat* (strait), and *teluk* (bay).

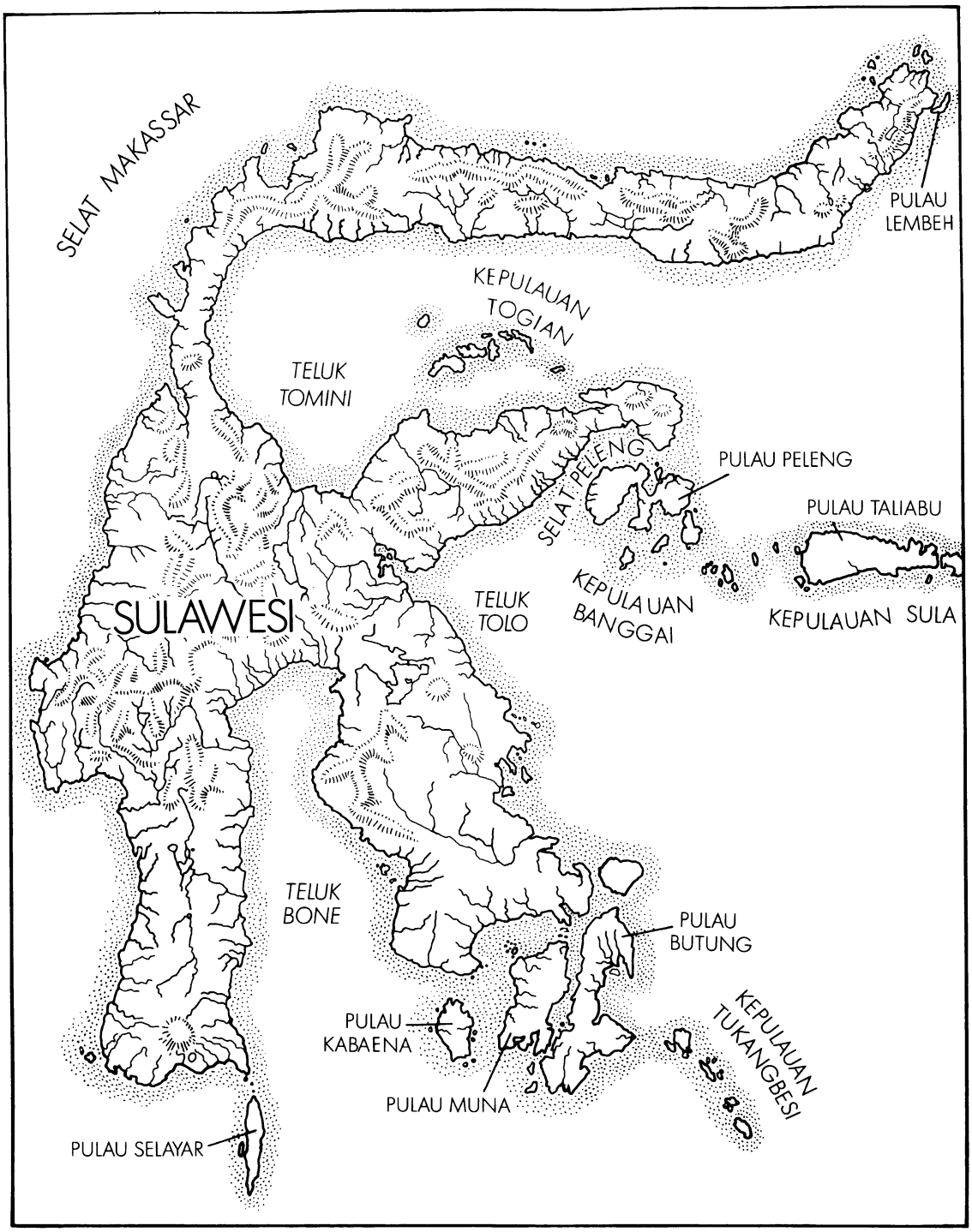


Fig. 4. Sulawesi, offshore islands, and nearby archipelagos.

ACKNOWLEDGMENTS

We could not have brought together the information recorded in this report without access to collections that are housed in museums located in five countries. To the curators of those institutions and members of their various support staffs, we are most grateful. We deeply appreciate their efforts not only in allowing us to examine material on the premises but in processing our requests for loans.

Other persons have contributed to our report in different ways. Linda K. Gordon provided some dental measurements taken from the type series of "*Rattus hoffmanni subditivus,*" which is stored in the National Museum of Natural History. Fran Stiles rendered the drawings of feet in figure 8, Patricia Wynne drew the diagrams (figs. 30 and 33) and the maps in figures 4 and 6, Shirley Chiu prepared figures 28 and 29, Peter Goldberg produced the photographs of skulls and toothrows, and Patricia Brunauer transformed too many rough drafts of typescript into clean manuscript with a word processor. Their contributions reflect skillful effort that has resulted in products defined by quality and style.

We could not have studied the new subfossil material reported here without the cooperation of D. J. Mulvaney. He sent Guy Musser the material collected in July and August 1969, during the archaeological expedition to the Makassar region of southwestern Sulawesi, a cooperative venture between members from the National Archaeological Institute of Indonesia and the Department of Prehistory at the Australian National University, Canberra (see Mulvaney and Soejono, 1970).

Charles J. Cole and Carol Townsend taught Guy Musser the techniques required to obtain chromosome spreads in the field, and generously allowed him access to equipment and supplies in their laboratory. The chromosomal spreads were photographed by Shirley Chiu.

Michael D. Carleton, James L. Patton, and Colin P. Groves read drafts of the manuscript. Their critical evaluations and suggestions for change contributed significantly to an improved and stronger final version, and we are indebted to them for their time and their helpful reviews.

Much of the material we studied from central Sulawesi was collected during Guy Musser's fieldwork there, an expedition that was supported by the Celebes Fund of the American Museum of Natural History as well as Archbold Expeditions, Inc. He was sponsored in Indonesia by the Lembaga Ilmu Pengetahuan Indonesia and the Museum Zoologicum Bogoriense, where Dr. Sampurno Kadarsan provided access to collections and extended every hospitality. Staff members of the Navy Medical Research Unit in Jakarta were unstinting in their efforts to provide Musser with any help he required.

Mary Ellen Holden was a Volunteer in the Department of Mammalogy at the American Museum of Natural History when she was collecting data for this report. She thanks the staff in the Volunteer Office at the American Museum for sponsoring her museum activities during that period.

This report is Number 119 in Results of the Archbold Expeditions.

THE *RATTUS HOFFMANNI* GROUP

The animal we have come to know as *Rattus hoffmanni* was first described by Dr. B. Hoffmann in 1887 (p. 18) under the name "Mus rattus var. celebensis n. var." Hoffmann's observations were based on a skin and skull of an adult female obtained from "Minahassa auf Nord Celebes," and it is his published description and drawing of the ventral view of the cranium (fig. 5) that now form our only information about the holotype. The type was kept in the Stäatliche Museum für Tierkunde in Dresden, but our queries to the staff there have resulted only in the disappointing report that the specimen could not be found in the collection, a fate apparently shared by at least some of the other holotypes that formed the basis of Hoffmann's new taxa (Musser, 1970). Fortunately, his careful description of the new variety "*celebensis*" clearly reflects the characteristics of the samples we have identified as *hoffmanni,* down to the texture and coloration of the fur as well as the number of mammae (eight, no pectoral pair). The chunky cranium, short and flaring zygomatic arches, in-

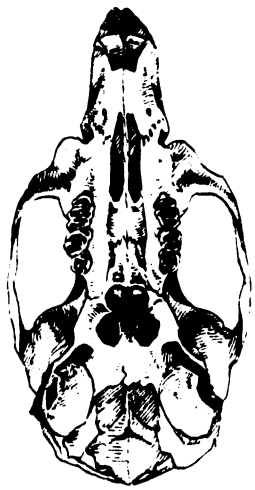


Fig. 5. Ventral view of the cranium that was part of the specimen upon which Hoffmann (1887) based his description of "*Mus rattus* var. *celebensis* n. var.," which Matschie (1901) later renamed "*Mus hoffmanni.*" Reproduced from the plate published in Hoffmann's report.

flated nasolacrimal capsules, sturdy zygomatic plates, wide molars, and divergent molar rows shown in Hoffmann's drawing are also common to specimens at hand from Sulawesi. We are confident that the rat described by Hoffmann and the animals in our samples represent the same species.

Although we are able to link the morphology of our material to Hoffmann's description of "*celebensis,*" we cannot apply Hoffmann's name to the species because it had already been used by Gray in 1867 in the combination *Mus celebensis* to designate a new species, also from Sulawesi. Thus, *celebensis* is the valid name for a distinctive species now placed in the genus *Taeromys* (Musser and Newcomb, 1983: 487). Recognizing this prior use of *celebensis,* Matschie (1901) renamed Hoffmann's variety as *Mus hoffmanni,* which to our knowledge is the oldest scientific name for the Sulawesian entity that in present-day taxonomic literature is referred to as *Rattus hoffmanni* (Ellerman, 1941, 1949; Laurie and Hill, 1954; Musser, 1987).

In addition to *R. hoffmanni,* we recognize another species in the *R. hoffmanni* group, *R. mollicomulus.* A small sample collected between 1100 and 2000 m on the slopes of Gunung Lompobatang near the tip of the southwestern peninsula of Sulawesi contains specimens with a phenotype distinct from the range of chromatic and morphological variation characterizing examples of *R. hoffmanni* obtained in the adjacent lowlands. That mountain form was described by Tate and Archbold in 1935 and named *Rattus mollicomulus.* Its range, as indicated by the few specimens now available for study, is confined to Gunung Lompobatang. *Rattus hoffmanni* and *R. mollicomulus* form one of several pairs of species occurring on the southwestern peninsula that sort out into complementary geographic ranges in which one encompasses mountain habitats and the other lowland.

In the pages to follow, we provide a gazetteer of collecting localities along with the specimens that we studied of both *R. hoffmanni* and *R. mollicomulus.* A diagnosis of *R. hoffmanni* is given next followed by a description, ecological observations, and an account of geographic variation and its reflection in taxonomy. We will also compare the morphological characteristics of *R. hoffmanni* with five other groups of *Rattus.* One consists of *R. mollicomulus*; our observations contrasting it with *R. hoffmanni* are detailed in the section where we discuss geographic variation among samples.

Another of these groups contains five species of *Rattus* that occur on Sulawesi but are not part of the fauna indigenous to the island. Their evolutionary histories are entwined with the evolution of mammalian faunas in other regions, probably mainland Asia, and their presence on Sulawesi most likely reflects distributional processes associated with human activity. Comparisons between this introduced component and endemic *R. hoffmanni* allow us to provide information by which examples of *R. hoffmanni* can be correctly identified in relation to the other species. We also affirm that the Sulawesi rat is a distinctive species with a separate evolutionary history and that it is part of a rodent fauna occurring solely on Sulawesi rather than an insular form of one of these other *Rattus.*

The third set of comparisons is between *R. hoffmanni* and *R. tawitawiensis,* which is native to Tawitawi Island in the Sulu Archi-

pelago north of Sulawesi between Mindanao and Borneo. These contrasts are important because the describers of the Tawitawi rat (Musser and Heaney, 1985) had noted morphological similarities between the two species, and we need to reaffirm that one is not just an island variety of the other.

Rattus elaphinus, known only from Pulau Taliabu in the Sula Archipelago between Pulau Peleng and the Malukus (fig. 4), is superficially similar to *R. hoffmanni* in some features related to body size, proportions, and skull conformation. The two species must be compared to document our assertion that *R. hoffmanni* is not represented in archipelagos to the east of Sulawesi by such species as *R. elaphinus.*

Finally, we compare *R. hoffmanni* with a new species endemic to Pulau Peleng, the largest island in Kepulauan Banggai (fig. 4). Those contrasts are provided when we diagnose and describe the new Peleng rat.

Gazetteer and Specimens

The 71 primary localities that comprise our samples are listed below and indexed by numbered dots on the map in figure 6. Some locales represent a single place; a few others also include nearby sites that are so close to the primary collection area that they could not be shown on such a large-scale map. Included for each locality are the specimens we studied, each identified by museum catalog number.

Rattus hoffmanni

1. **Teteamoet,** several miles southeast of Likupang, 0–100 m (1°40′N, 125°05′E): RMNH 21211, 21212; USNM 216816–216819, 216821, 216823–216827, 216829–216835, 216847, 216988–216992.
2. **Kampa** (probably refers to Gunung Kampi), 0–100 m (1°35′N, 124°53′E): USNM 200220–200223.
3. **Mapanget,** 0–100 m (1°32′N, 124°56′E): MZB 4000, 4001.
4. **Manado,** 0–100 m (1°30′N, 124°50′E): BM 7.1.1.84, 7.1.1.221, 97.1.2.42; MZB 1851, 4002.
5. **Kuala Prang,** 0–100 m (1°28′N, 125°14′E): USNM 217759.
6. **Gunung Klabat,** 5600–6500 ft (1°28′N, 125°02′E): USNM 217583, 217584, 217748–217751, 217752 (holotype of *Rattus mollicomus*), 217753–217758 (217749 and 217753 are at RMNH).
7. **Pulau Lembeh,** altitude of collection site is not recorded but highest point of island is 447 m (1°26′N, 125°13′E): FMNH 31843.
8. **Rurukan** (1°21′N, 124°52′E), 800 m: AMNH 101258. 3600 ft: BM 97.1.2.40, 97.1.2.41; ANSP 14168.
9. **Tonsealama** (also designated Tonsea), 600–700 m (1°19′N, 124°55′E): BM 40.534–40.552; MZB 4019, 4021, 4022.
10. **Tomohon,** 700–800 m (1°19′N, 124°49′E): MZB 4003, 4005–4008.
11. **Amurang,** 0–100 m (1°11′N, 124°35′E): MZB 1499, 4017, 4023; RMNH 2820, 2822, 2823.
12. **Tumaratus,** 700–800 m (1°09′N, 124°48′E): USNM 217760.
13. **Langgon** (also spelled Langowan), 700–800 m (1°09′N, 124°50′E): RMNH 21286.
14. **Temboan,** southwest of Gunung Soputan, 400–500 m (1°09′N, 124°40′E): USNM 217617, 217672, 217760–217763, 217785, 217893, 217894.
15. **Gunung Maujat,** 15 km east of Kotambogan, 1780 m (0°45′N, 124°25′E): SAM m12634, m12642.
16. **Dumoga-Bone National Park,** 3 km northeast of Toraut Danmi, 492 m (0°34′N, 123°54′E): SAM m12624–m12626.
17. **Dumoga-Bone National Park,** 1 km north of Gunung Mogogonipa, 250 m (0°27′N, 123°57′E): SAM m12618.
18. **Teluk Kuandang,** between Kuandang and Molinggapoto (Molengkopota), 0–100 m (0°50′N, 122°53′E): USNM 200075–200080, 200083–200090, 200166.
19. **Bumbulan,** 0–100 m (0°29′N, 122°04′E): AMNH 152987; MZB 4018, 4020, 5087, 5098.
20. **Sungai Paleleh,** 0–100 m (1°05′N, 121°55′E): USNM 200057, 200065, 200067, 200069–200071.
21. **Tolitoli,** 0–100 m (1°03′N, 120°49′E): USNM 200170, 200171, 200173, 200177, 200183, 200186–200189, 200191, 200193, 200194, 200196–200199, 200201, 200202, 200204, 200205, 200207–200209, 200211, 200214, 200215, 200217–200219.
22. **Labua Sore,** on east coast just north of Marantate, between Towera and Toboli, 0–100 m (0°37′S, 120°03′E): USNM 218007, 218088, 218089, 218093, 218106, 218108–218111, 218113, 218116, 218671, 218672.
23. **Bumbarujaba,** on road across peninsula from Tawaeli to Toboli, 500–800 m (0°43′S, 120°02′E): FMNH 43407, 43408; USMN 218094, 218095, 218097, 218098, 218100–

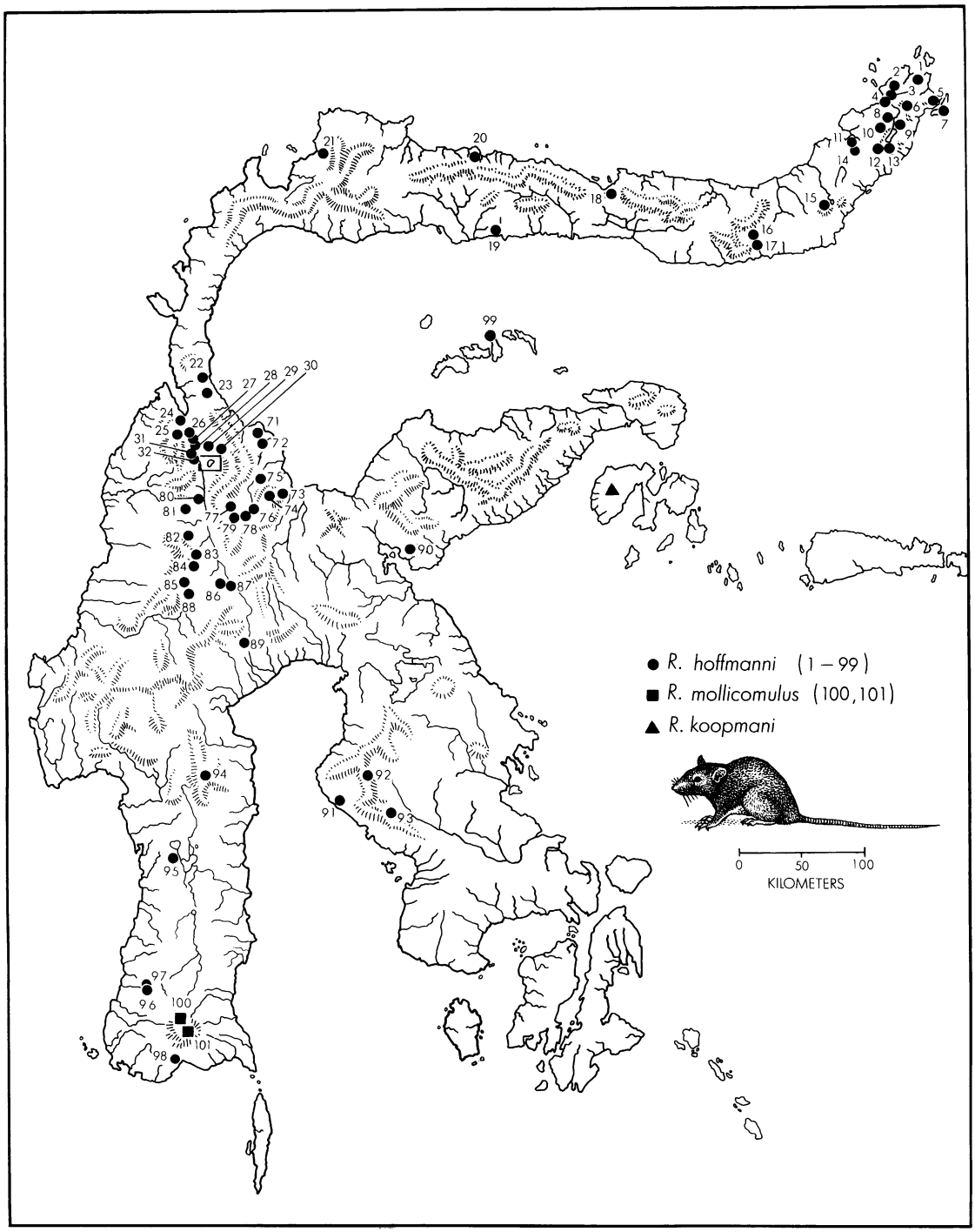
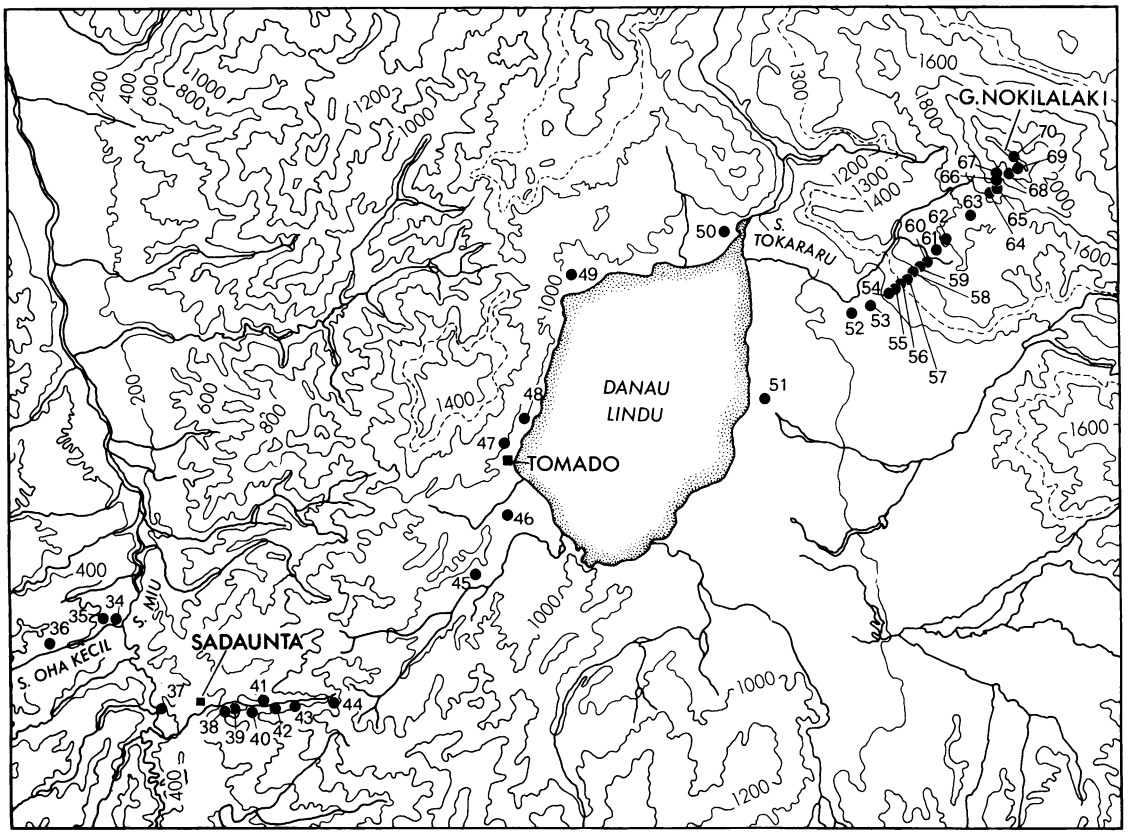


Fig. 6. Geographic distributions of *Rattus hoffmanni, R. mollicomulus,* and *R. koopmani,* n. sp. Numbered localities are listed in the gazetteer. The dashed contour line (see opposite map) at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane rain forest.



218105, 218129, 218130 (218102 and 218130 are at RMNH).

24. **Palu Valley, Rarapadende,** 80 m (0°56′S, 119°51′E): AMNH 229572.
25. **Palu Valley, Sibonu,** 45 m (1°00′S, 119°51′E): AMNH 229573, 229574.
26. **Palu Valley, Tulo,** 25 m (1°01′S, 119°53′E): AMNH 229576.
27. **Palu Valley, Kaleke,** 40 m (1°03′S, 119°52′E): AMNH 229557.
28. **Palu Valley, Deasi,** 75 m (1°05′S, 119°53′E): AMNH 229556. **Sidondo,** 40 m (1°05′S, 119°54′E): AMNH 229575.
29. **Puro Valley, Bobo,** 530 m (1°07′S, 120°01′E): AMNH 229555. **Makmur** and **Kapiroe,** 530 m (1°07′S, 120°02′E): AMNH 229538, 229558, 229560–229562. **Petimbe,** 530 m (1°08′S, 120°02′E): AMNH 229568–229571.
30. **Puro Valley, Bahagia,** 450 m (1°08′S, 120°06′E): AMNH 229554.
31. **Palu Valley, Leda,** 110 m (1°12′S, 119°44′E): AMNH 229559. **Pandere,** 110 m (1°12′S, 119°56′E): AMNH 229567.
32. **Palu Valley, Pakuli,** 110 m (1°14′S, 119°56′E): AMNH 229577–229579.
33. **Valley of the Sungai Miu, Omu,** 130 m (1°18′S, 119°57′E): AMNH 229563–229566.
34. **Valley of the Sungai Miu, Sungai Oha Kecil,** left side of Sungai Miu, 290 m (1°22′S, 119°57′E): AMNH 224948–224956.
35. **Sungai Oha Kecil,** 1100 ft: AMNH 224957.
36. **Sungai Oha Kecil,** 1500 ft: AMNH 224948.
37. **Sungai Miu (right side),** 350 m (1°23′S, 119°58′E): AMNH 224247–224250, 224260.
38. **Valley of the Sungai Miu, Sungai Sadaunta** (also spelled Sidaonta and Sidaunta), 675 m (1°23′S, 119°58′E): AMNH 224230–224246.
39. **Sungai Sadaunta,** 2500 ft: AMNH 224959. 2600 ft: AMNH 224960, 224961, 224983.
40. **Sungai Sadaunta,** 2700 ft: AMNH 224962–224965, 224970.
41. **Sungai Sadaunta,** 2800 ft: AMNH 224971, 224972. 2850 ft: AMNH 224973–224976, 224984–224987.
42. **Sungai Sadaunta,** 2900 ft: AMNH 224977, 224978. 2950 ft: AMNH 224979–224981.

43. **Sungai Sadaunta,** 3000 ft: AMNH 226825–226826.
44. **Sungai Sadaunta,** 3500 ft: AMNH 224982.
45. **Danau Lindu, Puroo** (also spelled Puro), 960 m (1°22′S, 120°02′E): AMNH 229558.
46. **Danau Lindu, Lombu** (also spelled Lembo), 960 m (1°20′S, 120°03′E): AMNH 229585–229587.
47. **Danau Lindu, Tomado,** 1000 m (1°19′S, 120°03′E): AMNH 223171–223191, 223193–223203, 223378, 223379, 223416, 223488–223490, 223763, 223764, 223971–223973, 224251–224259, 224261, 226930, 226940; MCZ 39599; USNM 218690, 218694, 218695, 218697–218699, 218799 (holotype of *Rattus hoffmanni linduensis*), 218201, 218703, 218705.
48. **Danau Lindu, Anca,** 960 m (1°19′S, 120° 03′E): AMNH 229589.
49. **Danau Lindu, Paku,** 950 m (1°17′S, 120° 03′E): AMNH 229581–229584.
50. **Danau Lindu, Bamba,** 950 m (1°17′S, 120° 06′E): AMNH 229581.
51. **Danau Lindu, Olu,** 955 m (1°19′S, 120°06′E): AMNH 223204–223206.
52. **Sungai Tokararu,** 12 km east-northeast of Palili (an abandoned village on the northeast shore of Danau Lindu), 1150 m (1°17′S, 120°07′E): AMNH 223380–223396, 223405–223408.
53. **Gunung Kanino** (1°17′S, 120°08′E), 3900 ft: AMNH 223397, 223491, 223492. 3920 ft: AMNH 223398, 223399, 223413. 3940 ft: AMNH 223400. 3950 ft: AMNH 223411.
54. **Gunung Kanino,** 4050 ft: AMNH 223414.
55. **Gunung Kanino,** 4150 ft: AMNH 223401, 223409, 223412, 223415.
56. **Gunung Kanino,** 4300 ft: AMNH 223402, 223403, 223410.
57. **Gunung Kanino,** 4500 ft: AMNH 223774. 4550 ft: AMNH 223404. 4600 ft: AMNH 223709, 223761.
58. **Gunung Kanino,** 4620 ft: AMNH 223762.
59. **Gunung Kanino,** 4750 ft: AMNH 223765, 225241. 4800 ft: AMNH 223710–223722, 223766, 223767.
60. **Gunung Kanino,** 4900 ft: AMNH 225717. 5000 ft: AMNH 223723–223728.
61. **Gunung Kanino,** 5200 ft: AMNH 223729–223733.
62. **Gunung Kanino,** 5300 ft: AMNH 225172.
63. **Gunung Nokilalaki,** 5700 ft (1°16′S, 120° 10′E): AMNH 223734, 223735.
64. **Gunung Nokilalaki,** 6300 ft: AMNH 223726, 223737.
65. **Gunung Nokilalaki,** 6400 ft: AMNH 223768, 225174. 6500 ft: AMNH 223738.
66. **Gunung Nokilalaki,** 6700 ft: AMNH 223739, 223740, 223769, 225175, 225176. 6800 ft: AMNH 223741–223744, 223770, 225178, 225179. 6900 ft: AMNH 225180.
67. **Gunung Nokilalaki,** 7000 ft: AMNH 225182, 225183. 7200 ft: AMNH 223745, 223746, 225184.
68. **Gunung Nokilalaki,** 7300 ft: AMNH 223747, 225185, 225186.
69. **Gunung Nokilalaki,** 7400 ft: AMNH 225187–225189, 225191–225193, 225203. 7450 ft: AMNH 223748.
70. **Gunung Nokilalaki,** 7500 ft: AMNH 223749–223760, 223771–223773, 225194–225199, 225200–225202.
71. **Malakosa, Kuala Navusu** (0°58′S, 120°27′E), 100 ft: AMNH 226025. 125 ft: AMNH 226026–226030. 130 ft: AMNH 226031, 226042. 150 ft: AMNH 226032, 226033. 200 ft: AMNH 226034. 250 ft: AMNH 226035, 226036. 300 ft: AMNH 225037. 350 ft: AMNH 226038. 400 ft: AMNH 226039. 500 ft: AMNH 226040. 700 ft: AMNH 226041.
72. **Tolai, Sungai Tolewonu,** 450 ft (1°04′S, 120°27′E): AMNH 226493.
73. **Pinedapa,** 100 ft (1°25′S, 120°35′E): USNM 219582, 219584, 219692.
74. **Rano Rano,** 1800 m (1°30′S, 120°28′E): USNM 219576–219579, 219583, 219585, 219586, 219588, 219590, 219614, 219617, 219618, 219621, 219623, 219632–219634.
75. **Napu Valley, Sedoa,** 1127 m (1°22′S, 120° 21′E): AMNH 229595.
76. **Napu Valley, Watutau,** 1048 m (1°34′S, 120°21′E): USNM 219615.
77. **Besoa Valley, Katu,** 1093 m (1°33′S, 120° 12′E): AMNH 229592.
78. **Besoa Valley, Rompo,** 1063 m (1°38′S, 120°18′E): AMNH 229593, 229594.
79. **Besoa Valley, Bariri,** 1152 m (1°42′S, 120°14′E): AMNH 229590, 229591.
80. **Kulawi,** 500 m (1°27′S, 119°59′E): USNM 218689.
81. **Gunung Lehio, Sungai Supoi,** 6166–7166 ft (1°33′S, 119°53′E): USNM 218674–218676, 218678, 218679.
82. **Kantewu,** 1000 m (1°42′S, 119°54′E): AMNH 229596–229599.
83. **Mamu,** 1060 m (1°56′S, 119°59′E): AMNH 229600–229603.
84. **Kalamanta,** 1100 m (1°57′S, 119°56′E): AMNH 226954, 229604, 229605.
85. **Sungai Kanatutu,** 1400 m (2°04′S, 119°54′E): AMNH 229608.
86. **Tedeboe** (2°06′S, 120°10′E), 1280 m: AMNH 229609. 1380 m: AMNH 226951.
87. **Dodolo,** 950 m (2°06′S, 120°15′E): AMNH 226953.
88. **Singkalong,** 1210 m (2°15′S, 119°58′E): AMNH 229606, 229607.
89. **Masamba,** 0–100 m (2°32′S, 120°20′E): BM

21.2.9.20; MZB 408, 4024–4026, 4028–4031; RMNH 21161, 21162.

90. **Sungai Ranu,** 10 m (1°51′S, 121°30′E): MZB 12173.
91. **Pegunungan Mekongga** (also called Mengkoka Gebirge), **Wawo,** 50 m (3°41′S, 121°02′E): AMNH 101062 (holotype of *Rattus hoffmanni mengkoka*).
92. **Pegunungan Mekongga, Tanke Salokko,** 1500 m: AMNH 101056, 101228, 101238. 2000 m: AMNH 101212.
93. **Pegunungan Mekongga, Masembo,** 550 m: AMNH 101063, 101064, 101066; MZB 4032, 4033.
94. **Uru, Pegunungan Latimodjang,** 2200 m (3°31′S, 119°56′E): AMNH 196575–196577.
95. **Tempe,** 0–100 m (4°08′S, 120°02′E): ZMA 12.673.
96. **Bantimurung,** 1–100 m (5°03′S, 119°41′E): AMNH 101289–101292, 101294.
97. **Leang Burung 1,** 0–100 m, a cave near the village of Pakalu, "about 2 km north of the main road from Maros, 10 km to the west" (Mulvaney and Soejono, 1970): AMNH 265045 (a subfossil edentulous fragment of right dentary).
98. **Batu Ejaya,** 275 m, a cave at the southern tip of the southwestern peninsula (see the map, description, and references in Mulvaney and Soejono, 1970): Subfossil Specimen Number 35, documented and figured in Musser (1984).
99. **Kepulauan Togian, Pulau Malenge,** exact collecting locality is unknown but highest part of the island is about 300 m (0°15′S, 122°03′E): AMNH 153320–153322, 153328, 153329, 153333, 153338, 153340, 153342, 153344–153347, 153350–153352; MZB 5890, 5895 (holotype of *Rattus biformatus*).

The following specimens of *R. hoffmanni* were studied but the places where they were caught were not mapped.

A. Minahassa District: RMNH 21213–21231.
B. Tamalanti, 3300 ft (see Laurie and Hill, 1954, for notes about this place): BM 40.553, 40.554, 40.603 (holotype of *Rattus tatei*), 40.604.
C. Bada Region: USNM 221058.
D. Kuala Besar: USNM 200061.
E. "Celebes": BM 40.555.

Rattus mollicomulus

100. **Lombasang** (also spelled Lambasang), northwest of Gunung Lompobatang, 1100 m (5°16′S, 119°50′E): AMNH 100995.
101. **Wawokaraeng, Gunung Lompobatang** (5°20′S, 119°55′E), 1500 m: AMNH 101134 (holotype of *Rattus mollicomulus*). 2000 m: AMNH 101191. **Piek van Bonthain,** or **Banta Eng** (Gunung Lompobatang), 2000 m (5°20′S, 119°55′E): BM 97.1.3.11, 21.2.9.23.

Rattus hoffmanni (Matschie)

Mus rattus var. *celebensis* Hoffmann, 1887: 18 (not the *Mus celebensis* of Gray, 1867; type locality, Minahassa, northeastern Sulawesi; holotype may be lost).

Mus hoffmanni Matschie, 1901: 284 (a renaming of Hoffman's variety "*celebensis*").

Rattus hoffmanni linduensis Miller and Hollister, 1921: 70 (type locality, Tomado, 1000 m, central Sulawesi; holotype, USNM 218799).

Rattus mollicomus Miller and Hollister, 1921: 71 (type locality, Gunung Klabat, 6500 ft, northeastern Sulawesi; holotype, USNM 217752).

Rattus hoffmanni mengkoka Tate and Archbold, 1935: 3 (type locality, Wawo, 50 m, southeastern Sulawesi; holotype, AMNH 101062).

Rattus biformatus Sody, 1941: 307 (type locality, Pulau Malenge, Kepulauan Togian; holotype, MZB 5895).

Rattus tatei Ellerman, 1941: 215 (type locality, Tamalanti, 3300 ft, central Sulawesi; holotype, BM 40.603).

Emended Diagnosis

The following combination of characteristics distinguishes *Rattus hoffmanni* from any other described species of *Rattus*: (1) moderate body size; (2) tail monocolor and about as long as head and body; (3) brown feet; (4) large and brown ears; (5) soft and dense fur with short and inconspicuous guard hairs; (6) brown upperparts, gray to buffy gray underparts; (7) eight mammae (usually no pectoral pair); (8) smooth and beveled interorbital margins; (9) narrow incisive foramina; (10) moderately inflated bullae; (11) wide molars relative to cranial proportions; (12) molar rows divergent posteriorly; (13) cusp t3 on first molar large and distinct from cusp t2; (14) cusp t3 on second and third molars either very small or absent; (15) anterior cingulum of first upper molar in form of shelflike ridge; (16) posterior cingulum of first upper molar present in about half of any sample; (17) no anterocentral cusp at front of first lower molar; (18) karyotype with 2N of 42, FN of 62 (females) and 61 (males), medium-sized subtelocentric X-chromosomes; (19) diet frugivorous; and (20) habitat cool and wet tropical evergreen lowland and montane forests.

Distribution

Places on Sulawesi and offshore islands where our samples originated are shown on the map in figure 6. Known localities cluster in the northeastern tip and the northern portion of the central region of Sulawesi, reflecting the areas where activities of collectors have been most intense. *Rattus hoffmanni* is certainly more widespread than indicated by the scatter on the map; judged from Musser's experience working with the species in its natural habitat, we think its distribution includes all of mainland Sulawesi, except Gunung Lompobatang, wherever there is suitable habitat (primary and secondary forest, scrub adjacent to forest). That it will also be found on all islands just off the coast is a speculation we are less willing to support. Insular collections of *R. hoffmanni* come from Pulau Lembeh off the coast of the northeastern peninsula, and from Pulau Malenge in the Togian islands. Populations will probably be found elsewhere, such as the large islands that form the southeastern tip of Sulawesi, but perhaps not other smaller islands where the combination of island size, habitat characteristics, and geologic history may have formed barriers to the species.

The vertical distribution of *R. hoffmanni* on mainland Sulawesi is impressive. Collections from most of the arms and from the central core of the island span an altitudinal range that extends from just above sea level to 2000–2300 m (table 18); those highest elevations often indicate mountain summits. The entire range brackets different tropical evergreen forest formations and ambient environmental regimes. Most of the other species of murids endemic to Sulawesi are closely tied to a particular forest type and thus have a more restricted altitudinal distribution than does *R. hoffmanni* (tables 17, 18).

Description

External Form: Adult and young adult *Rattus hoffmanni* are chunky and brown, with a tail about as long as the head and body (figs. 7, 8; tables 5, 6) and a body weight exceeding 90 g but usually not 250 g (the weights from a sample obtained in central Sulawesi and listed in table 2 are representative). The soft, short, and dense dorsal coat is composed of underfur, overfur, and guard hairs. Unpigmented or tipped with buff, the filamentous underhairs are hidden within the overfur, which may be as long as 20 mm. Each hair in the overfur has a gray base, middle black band, and a buffy band that tips some shafts or lies beneath a black tip in others. Scattered through the coat are thin, flexible, and translucent semirigid hairs that do not extend beyond the overfur and are not stiff enough to alter the soft texture of the pelage. Guard hairs project past the overfur layer by only 5–10 mm and are inconspicuous; the basal half of each is unpigmented or pale gray, the distal half black. Pigmented bands of the different layers combine to render the dorsal coat an overall rich brown speckled with buff and black. The midline of the head and body is slightly darker than the sides, both because of the concentration of guard hairs along the middorsal region and because of the wider buffy bands of hairs in the fur covering lateral portions of the body.

Color of the upperparts varies. In almost every large series some specimens are dark—brownish black highlighted with buff—and others are much paler—brownish yellow or tawny speckled with black—but dark brown characterizes most rats. We have not encountered any albinistic or melanistic individuals among the samples studied.

Fur clothing underparts of the head and body is short (5–10 mm long), soft, and thick. Coloration varies from silver gray tinged with pale buff to rich dark buff underlain by dark gray. In those specimens with mostly gray venters, the hairs have gray bases and unpigmented tips. Hairs on the chest are tipped with buff and that tinge extends as a streak along the midventral line onto the abdomen. Hairs have gray or dark gray bases and deep buffy distal portions in those rats characterized by intense buffy underparts. In these the entire venter is buff, not just the pectoral region. Ventral fur coloration of most specimens fall between these two extremes, but the entire range of variation is present within any large sample obtained from a single locality. A white patch on either chest or inguinal region is present on some animals, but the occurrence in samples is rare. More common is a chestnut stain on throat and chest of adults (not seen on juveniles) in series col-

TABLE 2

External Measurements (in millimeters) and Weight (in grams) from a Sample of *Rattus hoffmanni* Obtained along Sungai Sadaunta, 2228–3500 Feet, in Central Sulawesi

(Mean and range [in parentheses] are provided for each measurement. Specimens are in AMNH.)

Age and sex	Sample size	Length				Weight
		Head and body	Tail	Hind foot	Ear	
Adults						
Females	11	**182.1** (175–193)	**173.4** (155–187)	**38.4** (36–41)	**22.6** (22–23)	**153.8** (130–175)
Males	13	**193.1** (182–211)	**178.6** (162–192)	**39.8** (37–42)	**22.7** (22–24)	**187.2** (155–240)
Young adults						
Females	5	**177.6** (169–185)	**164.0** (160–170)	**38.6** (37–40)	**23.0** (22–24)	**115.0** (95–140)
Males	7	**179.8** (167–195)	**175.3** (155–195)	**40.0** (38–42)	**22.8** (21–24)	**158.7** (120–210)
Juveniles						
Females						
224976		124	113	33	20	60
224972		120	97	31	19	37
224973		108	95	30	19	33
Males						
224974		101	95	29	18	30

lected at all altitudes sampled, from coastal plain to mountaintop.

Mystacial, submental, superciliary, genal, and interramal vibrissae (see Brown, 1971, for descriptions of vibrissae and terminology) adorn the head. The interramal and submental hairs lack pigment; vibrissae in the other sets are glossy black. A blackish ring encircles each eye. The ears are large (about 13% of length of head and body), have a rubbery texture in life, and are dark, ranging from grayish brown to brownish black. The pinnae appear naked, but are actually covered (inside and out) with fine, very short hairs.

Upper surfaces of the front and hind feet, including digits, are brown on most specimens: the hair cover is brown as well as the integument itself (the color appears solid in most museum specimens, but in life the feet are dark speckled brown). A few individuals have silver highlights due to unpigmented hairs scattered through the brown ones, and some have speckled grayish brown dorsal surfaces. In all rats the lateral half of each carpal and metacarpal region is darker than the medial half. All claws are cream-colored and each is overlaid by a tuft of silver hairs. Palmar surfaces are naked and either unpigmented or pale gray. Plantar areas are also without hair and range from gray to brown, sometimes dark brown. Three prominent interdigital pads and two larger metacarpal mounds cover each palm (fig. 9). Unpigmented ulnar carpal vibrissae form a tuft below each wrist. Beneath each long and slender hind foot, interdigital pads 1 and 4 are posterior to pads 2 and 3, the thenar pad is thick and elongate, and the smaller hypothenar is large and oval (fig. 9). (See Brown and Yalden, 1973, for description and terminology of pads.)

The tail is dark brown (often a glossy chocolate tone; grayish brown in a few) and about the same length as head and body (sometimes shorter, but rarely longer) (tables 2, 5, 6). It is trapezoidal in cross section, not round. There are 9–12 circles of epidermal scales per centimeter in adults (counted one-third the distance from the tail base). The scale rings overlap and each scale supports three hairs, the usual condition in species of *Rattus*. Most hairs are as long as two scales, and their combined cover imparts a finely haired appearance to the tail.

Females have eight functional teats—one postaxillary pair, one abdominal pair, and two inguinal pairs. This number and their position are characteristic of females in nearly all samples; the exceptions are two specimens from Pulau Malenge that have a pec-

Fig. 7. Adult *Rattus hoffmanni* from primary forest near the village of Tomado, 1000 m.

toral pair in addition to the other four. Those teats, however, are tiny and were probably not connected to mammary tissue when the rats were alive; the other teats by contrast are large and were obviously functional. A specimen from Bantimurung, on the southwestern peninsula of Sulawesi, also has a vestigial pair of pectoral teats.

Young rats in full juvenile pelage weigh less than 70 g (table 2), and their fur is finer and darker than that of adults. Fur over the upperparts is 8–10 mm long, dense, and very soft. The hairs have dark gray bases and buffy tips, producing an overall effect of dark brown along the top of the head and body; the sides are paler. The ventral coat is composed of fine, soft hairs and the range in color is similar to that found among adults. Ears are glossy, blackish brown, and dorsal surfaces of front and hind feet are usually very dark brown.

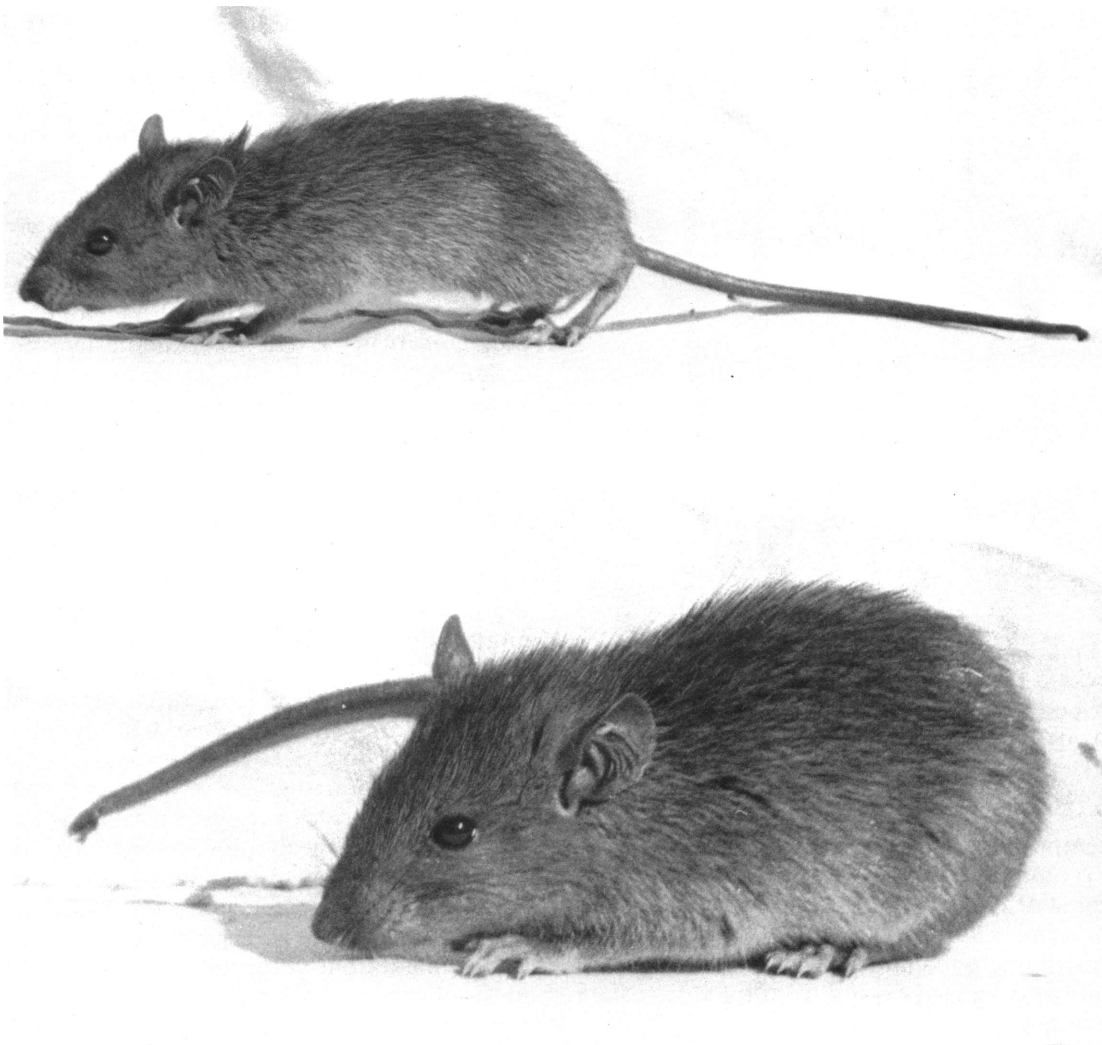


Fig. 8. Views of *Rattus hoffmanni*. The rat was caught in disturbed primary forest next to Tomado.

CRANIUM: Dorsal, ventral, and lateral cranial aspects of *R. hoffmanni* are illustrated in figure 10, and morphological details are enlarged in figure 12. From a dorsal perspective, the cranium has a moderately long and wide rostrum; the thin bony inflations over the nasolacrimal spaces are especially conspicuous. Behind each nasolacrimal capsule, the deep zygomatic notch reflects a wide zygomatic plate in which the projecting anterior spine extends forward to the posterior margin of the capsule or far enough to cover at least half of the inflated capsule. The posteroventral portion of the plate is thick and massive and sits above most of the first molar. The interorbit is wide in adults, and its dorsolateral margins are smooth and beveled in most specimens. These rounded edges transform posteriorly into thick ridges that sweep out and back in an ovate outline to the lambdoidal ridges, defining in high relief the dorsolateral rims of the postorbital and temporal regions. The sides of the braincase are not vertical, but slope outward slightly from the

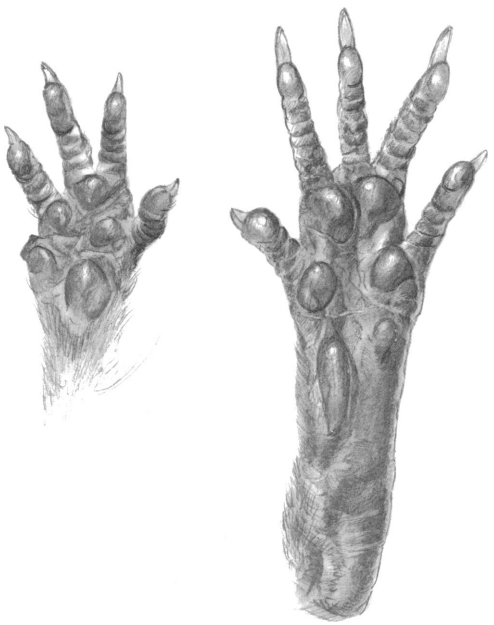


Fig. 9. Left front and hind feet of *Rattus hoffmanni* (AMNH 240504). **Left:** Palmar surface. **Right:** Plantar surface; note the four large interdigital pads, the elongated thenar and the small hypothenar mounds.

temporal ridges to the squamosal roots of the zygomatic arches. A wide interparietal forms most of the dorsal surface of the occiput; the anterior margin of the latter is marked by rough and wide lambdoidal ridges. Solid zygomatic arches bow out from the sides of the braincase.

Viewed in ventral aspect, the chunky rostrum, inflated nasolacrimal capsules, and wide zygomatic plates are prominent. Incisive foramina are shorter than the diastema, are narrow, and project between the first upper molars in all specimens, but rarely extend beyond the anterior lingual roots of those teeth (fig. 12B). The wide and long bony palate is developed into a shelflike extension projecting up to 2 mm past the molar rows. It is pierced by posterior palatine foramina opposite where the second molars overlap the third molars. The toothrows are not parallel, but diverge posteriorly, which contributes to the spacious aspect of the bony palate. Large sphenopalatine vacuities in the roof of the mesopterygoid fossa extend along the anterior portion of the basisphenoid and continue beside the presphenoid. The pterygoid fossae are moderately excavated, and each plate is perforated by a large sphenopterygoid vacuity (fig. 12B) and an opening through which the foramen ovale is evident. The anterior part of this hole is the posterior opening of the alisphenoid canal (fig. 12B). That entity, along with a groove just medial to the ridgelike margin of the pterygoid plate, reflects a cephalic circulatory pattern common to species of *Rattus* (Musser, 1982a). Back of each pterygoid plate is the wide middle lacerate foramen, and posterior to that are moderately inflated bullae; their bony eustachian tubes are wide and short.

In side view, the cranium resembles that of other species of *Rattus* (fig. 10). The dorsal outline of the skull is convex, the nasals project slightly beyond the anterior margins of the premaxillaries, and the occiput bulges past the lambdoidal ridges and out over the occipital condyles. The partial concealment of the inflated nasolacrimal capsule by a wide zygomatic plate is evident, as is the robust zygomatic arch and prominent hamular process anterior to the auditory bulla. A wide postglenoid foramen that is confluent with the middle lacerate opening separates the auditory bulla from the squamosal and alisphenoid bones (fig. 12A). Above the bulla, the squamosal is intact, not perforated by a squamoso-mastoid (subsquamosal) foramen. The configuration of the side of the cranium in the alisphenoid region dorsal to the rim of the pterygoid plate is typical of species of *Rattus* (Musser, 1982a; Musser and Newcomb, 1983): an alisphenoid strut is not present, and the cavity represents coalescence of the foramen ovale accessorius with the buccinator-masticatory foramina. The small opening at the front of the depression is the anterior opening of the alisphenoid canal, and the larger hole at the back is the foramen ovale (fig. 12A). The masticatory and buccinator branches of the maxillary nerve emerge from the foramen ovale. The infraorbital branch (internal maxillary) of the stapedial artery passes along the bottom of the open alisphenoid canal, through the anterior opening, and then into the orbit through the anterior alar fissure; this bony configuration and cephalic arterial pattern are common to many species of muroid rodents (see the il-

lustrations in Carleton and Musser, 1989). A large paroccipital process (often missing in poorly prepared skulls) juts down behind each bulla.

MANDIBLE: The mandible of *R. hoffmanni* is represented by a dentary shown in figure 10. It is a robust element and has a high falciform coronoid projection and a deeply concave margin between condyloid and angular processes. The incisor capsule forms a prominent bulge below the coronoid. In outline, relative positions of foramina and masseteric ridge, and surface sculpture, the dentaries resemble those of other species of *Rattus*.

DENTITION: The upper and lower incisors are wide and appear sturdy, and their enamel layers are deep orange. The upper pair curves back toward the molars (opisthodont), the usual form in species of *Rattus*. Also shared with other *Rattus* are *R. hoffmanni*'s pattern of multiple molar roots (fig. 13). Beneath each first upper molar is a large anterior root, a small labial, large posterior, and two medium-sized lingual roots. The second molar is held by four roots of about equal size, and each third molar has two small anterior roots along with a posterior anchor that is wide and sturdy. Large anterior and posterior roots joined with smaller labial and lingual ones hold each first lower molar. Each second and third lower molar has a pair of small anterior roots and a chunky, wide posterior one. Other dental similarities between *R. hoffmanni* and most *Rattus* species are the shape and size (length and width) of each molar relative to others in the row, extent of overlap among teeth in each molar row, heights of crowns and cusps, and the close proximity of cusp rows to one another on each tooth (Musser, 1981a, 1982a).

The upper molars of *R. hoffmanni* are wide (tables 5, 6) and chunky (figs. 14, 15) in relation to cranial dimensions. The cingular face of each first upper molar is outlined by either a prominent ridge or a shelf, which supports cusplets in some specimens (figs. 15, 28). These distinctions set the species apart from many other *Rattus*, particularly *R. rattus* and its relatives. The occlusal patterns formed by cusp rows, however, resemble the basic patterns seen in most species of *Rattus* (Musser, 1981a; Musser and Newcomb, 1983; Musser and Heaney, 1985), and the molar views in figure 14 portray the cusp conformation common to most specimens of *R. hoffmanni* that we have examined. The patterns are simple. Cusp t3 on the first tooth is large and conspicuous in all specimens (the comparable cusp in samples of *R. norvegicus* and *R. nitidus*, for example, is either absent or only weakly expressed). We have never found a cusp t7, which is responsible for part of the coronal complexity in other murines (Musser and Newcomb, 1983), on any of the upper molars among the specimens studied. Frequencies of occurrence of cusp t3 on second and third molars and degree of expression of the posterior cingulum on the first molar are the noticeable features that vary in the samples.

To estimate the variation of cusp t3, we examined 137 specimens collected at altitudes from near sea level to above 2000 m in the central part of Sulawesi. We recorded whether cusp t3 was present or absent only from specimens in which the teeth were slightly or moderately worn. Of 137 such specimens, 73 (53%) have a cusp t3 on each second molar and 64 (47%) lack it; 38 (28%) have the cusp on each third molar and 99 (72%) do not. The cusps are usually very small, an enamel nubbin on the cingular ridge (something like that in fig. 15A, for example), a structure that outlines the anterolabial margin of the second and third molars of all specimens; only in a few individuals does cusp t3 form a prominent part of the anterolabial margin of each tooth (see fig. 15C, for example). The topographic effect is that the anterolabial margin of each second and third molar in most specimens either is cuspless or appears so even when a cusp exists because it is usually such a small and insignificant part of the cingular ridge.

A posterior cingulum is present on the first upper molars in 64 (47%) rats of the 137 from central Sulawesi, but is not developed on either the second or third upper molars. Without a posterior cingulum, the rear margin of the first molar resembles that shown in figure 15D, in which the backs of cusps t8 and t9 give the molar a convex posterior outline that is either smooth or interrupted by only a slight bulge. When present, the posterior cingulum is usually expressed as one of the configura-

Fig. 10. Views (×2) of the cranium and dentary of an adult *Rattus hoffmanni* (AMNH 224248) from central Sulawesi.

Fig. 11. Views (×2) of the cranium and dentary of the young adult holotype of *Rattus koopmani*, n. s., from Pulau Peleng.

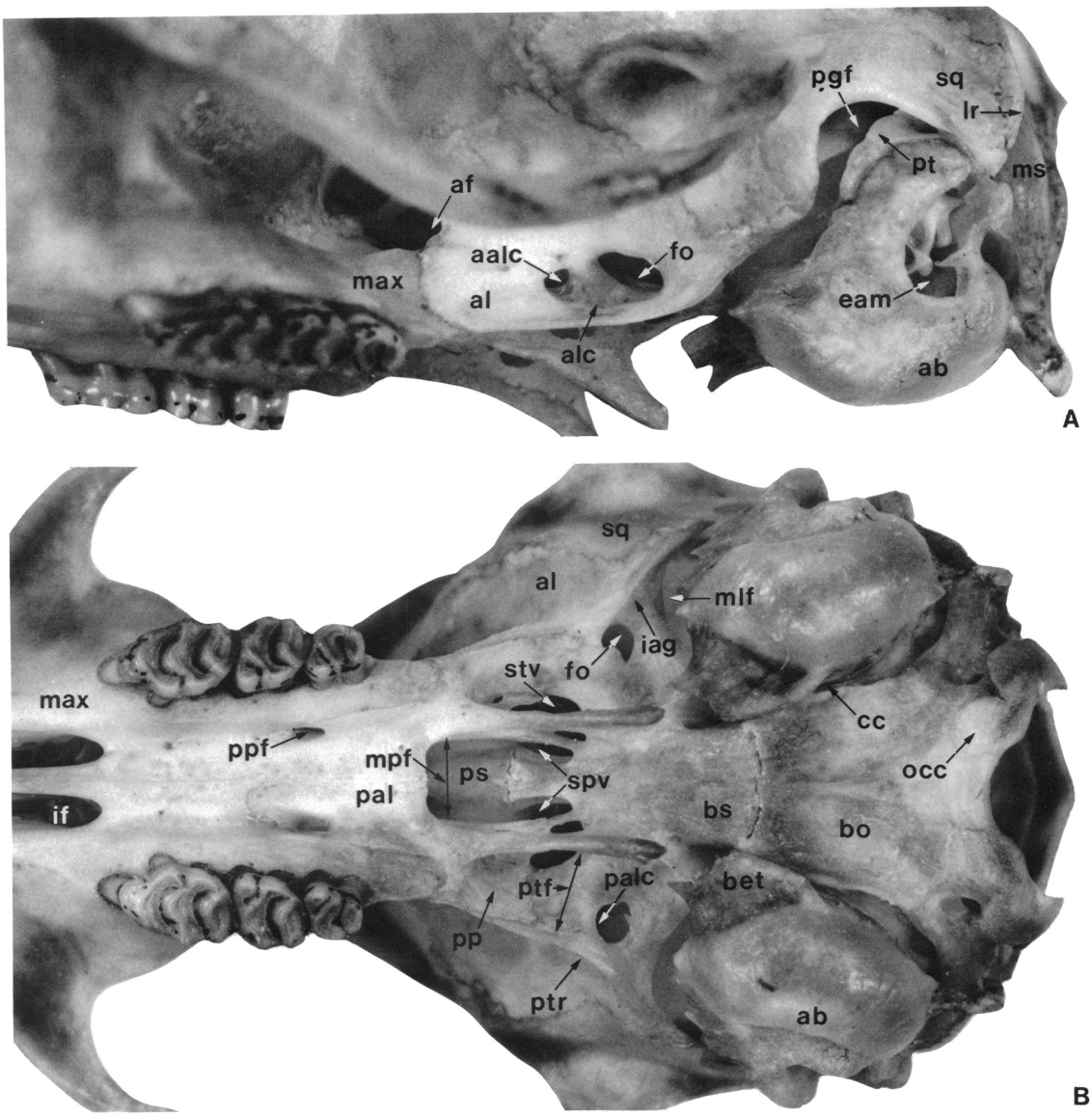


Fig. 12. Lateral (A) and ventral (B) cranial views of *Rattus hoffmanni* (AMNH 224248). **aalc,** anterior opening of alisphenoid canal; **ab,** auditory bulla; **af,** anterior alar fissure; **al,** alisphenoid; **alc,** alisphenoid canal; **bet,** bony eustachian tube; **bo,** basioccipital; **bs,** basisphenoid; **cc,** carotid canal; **eam,** external auditory meatus; **fo,** foramen ovale; **iag,** groove for the infraorbital branch of the stapedial artery; **if,** incisive foramina; **lr,** lamboidal ridge; **max,** maxillary; **mlf,** middle lacerate foramen; **mpf,** mesopterygoid fossa; **ms,** mastoid portion of the petromastoid; **occ,** occipital condyle; **pal,** palatine; **palc,** posterior opening of the alisphenoid canal (the infraorbital branch of the stapedial artery enters the braincase [where the arrow points] dorsal to the pterygoid); **pgl,** postglenoid foramen; **pp,** pterygoid plate; **ppf,** posterior palatine foramen; **ps,** presphenoid; **pt,** periotic; **ptf,** pterygoid fossa; **ptr,** pterygoid ridge; **sq,** squamosal; **spv,** sphenopalatine vacuities; **stv,** sphenopterygoid vacuity.

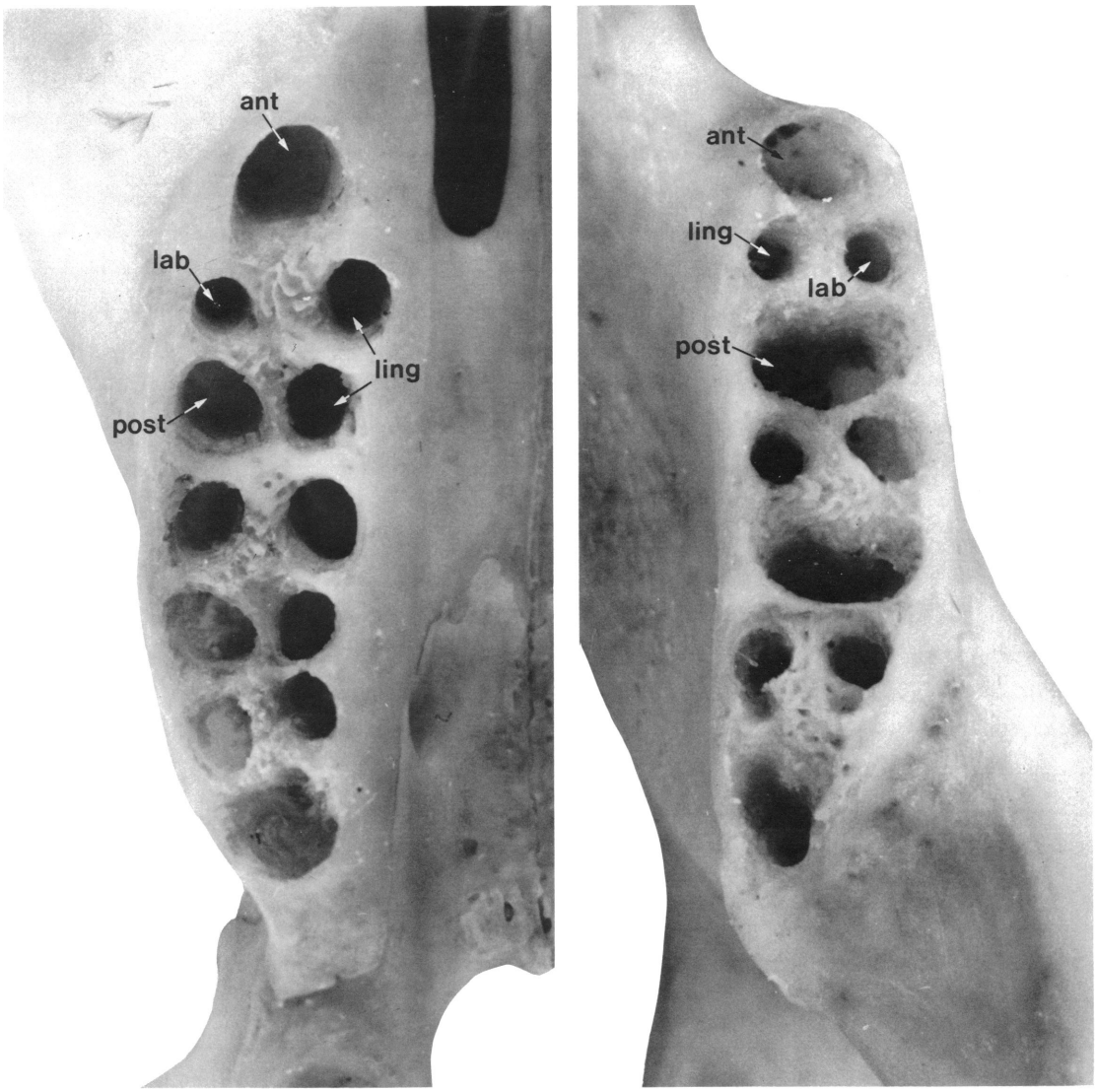


Fig. 13. Views (×12) of alveoli for right molar roots of *Rattus hoffmanni* (AMNH 223095). **Left:** Ventral view of upper alveoli (numbers of alveoli per molar are, from top to bottom, 5, 4, and 3, respectively). **Right:** Dorsal view of lower alveoli (4, 3, and 3, respectively). **ant,** alveolus for anterior root; **lab,** labial; **ling,** lingual; **post,** posterior.

tions shown in figure 15, in which the range extends from a discrete enamel cusp with a minute dentine center (fig. 15A) to an angular ridgelike labial projection (fig. 15C). The high frequency and prominent development of the posterior cingulum in *R. hoffmanni* are unusual compared with the occurrence and expression of this structure in most other species of *Rattus* (Musser, 1981a; Musser and Newcomb, 1983).

Other than their width and chunky aspect, the lower molars of *R. hoffmanni* resemble those in samples of other species of *Rattus* in the conformation of occlusal patterns formed by cusp rows and associated cusplets (fig. 16). The cusp patterns, like those of the

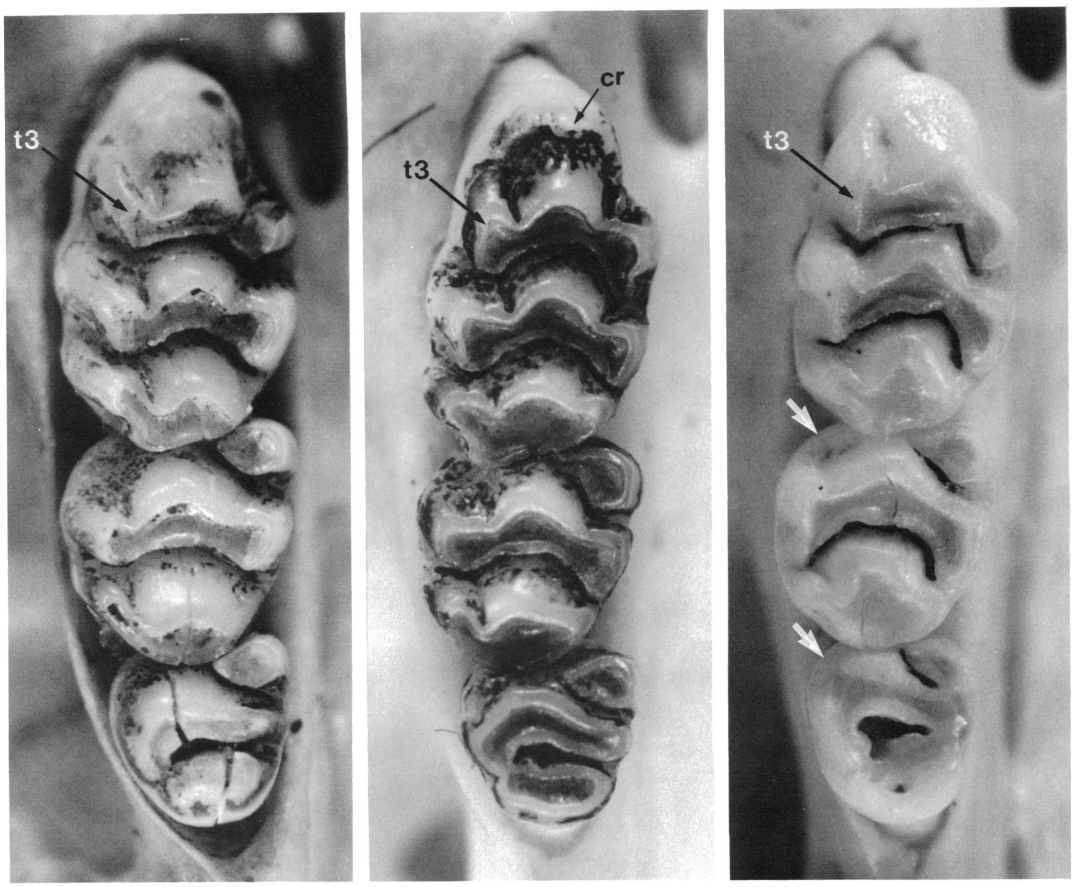


Fig. 14. Occlusal views of right upper molar rows. **Left:** *Rattus hoffmanni*, young adult (AMNH 224957; CLM1–3 = 7.2 mm). **Middle:** *R. hoffmanni*, adult (AMNH 223180, CLM1–3 = 7.6 mm). **Right:** Holotype of *R. koopmani*, n. sp., young adult (AMNH 109203; CLM1–3 = 8.7 mm). Cusp t3 on M1 is large and a prominent component in all three toothrows. *Rattus koopmani* lacks cusp t3 on M2 and M3 (white arrows). Note the anterior cingular ridge (**CR**) with its pimplelike cusplet on the front face of M1 in AMNH 223180.

upper molars, are simple. The anterior lamina of the first molar, for example, consists of anterolingual and anterolabial cusps only; an anterocentral cusp, which is such a frequent and prominent feature of the occlusal pattern in some species (*Rattus everetti* is one; Musser and Newcomb, 1983: 519, fig. 92), is absent from all the specimens of *R. hoffmanni* available to us. The slight complexities that exist in what are otherwise simple chevronlike rows of cusps are expressed by the presence of labial cusps and cusplets. All 137 animals from central Sulawesi have a posterior labial cusplet on each first and second molar. An anterior labial cusplet was found on the first molar in all specimens but one. An anterolabial cusp occurs on each second molar in all 137 specimens and on the third in all but two individuals. Labial cusps and cusplets are basically a fixed component on the occlusal surfaces of lower molars in *R. hoffmanni*.

CHROMOSOMES: We analyzed chromosomes from nine males and six females of *R. hoffmanni*. **Males:** AMNH 226039 (Kuala Navusu, 400 ft); AMNH 224240, 224983, 224984 (Sungai Sadaunta, 675 m, 2600 ft, and 2850 ft, respectively); AMNH 223182, 223185, 223488 (Danau Lindu, Tomado, 1000 m); AMNH 223709, 223766 (Gunung

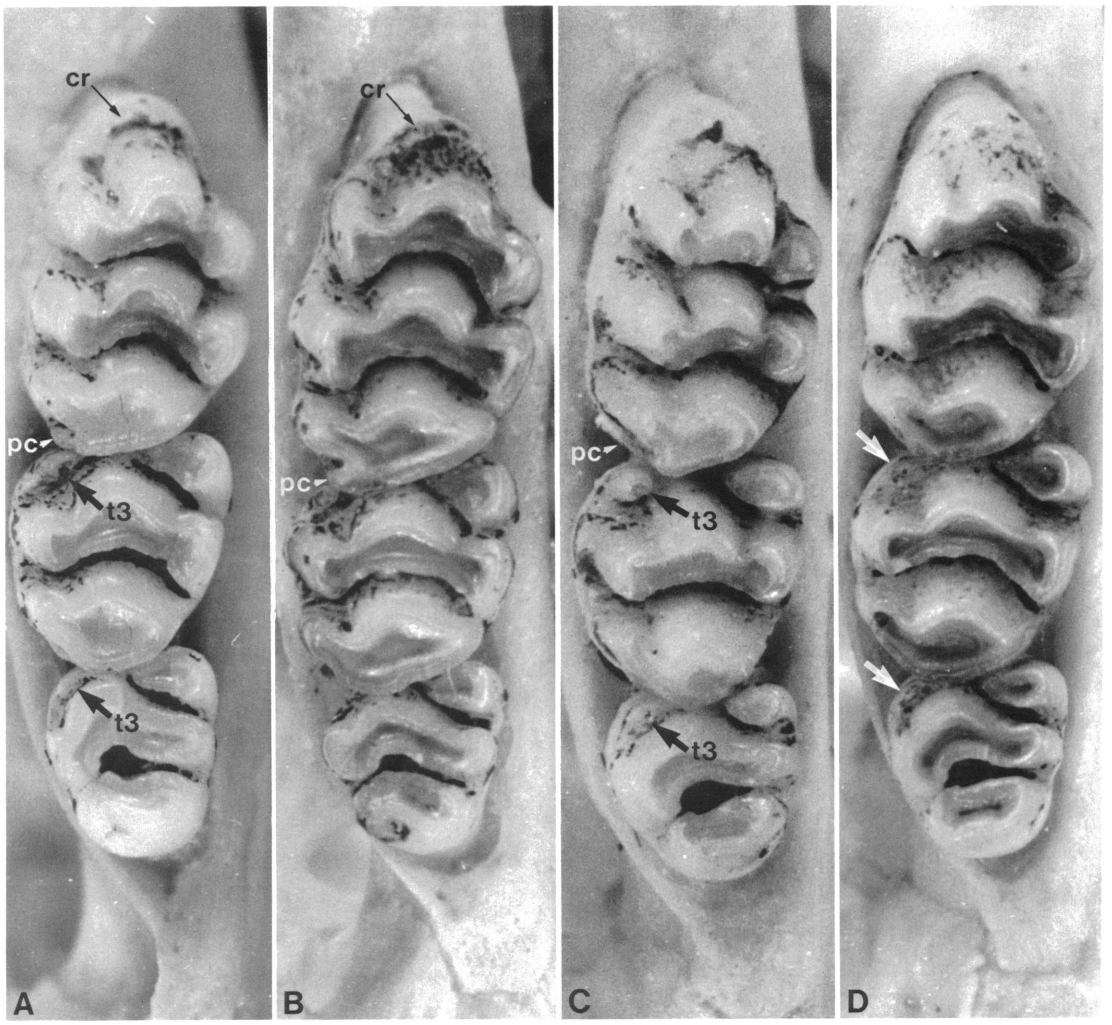


Fig. 15. Occlusal views (×13) of right upper molar rows of *Rattus hoffmanni* showing variation in expression of the posterior cingulum (**pc**) and cusp t3. **A.** The posterior cingulum as a prominent cusplike labial projection (AMNH 224961). **B.** The appearance of a large posterior cingulum in a worn molar (AMNH 223383). **C.** A reduced posterior cingulum expressed as a posterolabial ridge (AMNH 224252). **D.** No posterior cingulum at the back of the molar (AMNH 223171). Look also at the variation of cusp t3 on the second and third molars. Each may be a small bump on the anterolabial ridge (**A**) or a small but prominent cusp (**C**), or absent (**D**; white arrows). Note the cingular ridge (**cr**) outlining anterior margin of M1 in **A** and **B**.

Kanino, 4600 ft and 4800 ft, respectively). **Females:** AMNH 224236, 224239 (Sungai Sadaunta, 675 m); AMNH 223190, 223191 (Danau Lindu, Tomado, 1000 m); AMNH 223765, 223720 (Gunung Kanino, 4750 ft and 4800 ft, respectively). Samples of a male karyotype and of a female are illustrated in figure 17.

In all 15 animals, the diploid number is 42; the fundamental number is 61 for the males and 62 for the females. The autosomal complement in each male consists of 1 pair of large subtelocentrics, 1 pair of small subtelocentrics, 7 pairs of medium-sized to small metacentrics, and 11 pairs of telocentrics that grade in size from large to small. We presume

Fig. 16. Occlusal views of right lower molars of same specimens illustrated in figure 13. **Left:** *Rattus hoffmanni* (clm1–3 = 7.4 mm). **Middle:** *R. hoffmanni* (clm1–3 = 7.4. mm). **Right:** *R. koopmani*, n. sp. (clm1–3 = 8.5 mm). Note absence of anterocentral cusp (arrow at top of each toothrow) but presence of full complement of labial cusps and cusplets (other arrows) in all three specimens.

that a subtelocentric chromosome and telocentric one, both of medium size, form the X and Y sex elements. Each female has a pair of medium-sized subtelocentrics, which we assume to be the X-chromosomes; the remaining chromosomes in the karyotype are similar to those of the males, both in number of kinds and gradations in size.

Our results differ from those reported by Duncan (1976), who examined spreads obtained from a female *R. hoffmanni* collected from Tomado on the shore of Danau Lindu. He noted only one pair of subtelocentrics ("submetacentric" was his term), and assumed that the male and female sex chromosomes were both telocentric ("acrocentric"). We did not encounter this kind of variation in the chromosomal spreads from any individual in our sample, and we suspect the contrasting results to reflect the metaphase quality of the preparations.

There is little difference in chromosome morphology between our samples of *R. hoffmanni* and those of most of the other species analyzed that we would regard as members of the genus *Rattus* (table 3). The Philippine *R. everetti,* Indochinese *R. sikkimensis* (referred to as *R. sladeni* in the chromosomal literature), Asian *R. turkestanicus,* and Sundaic *R. tiomanicus* are possibly the most distant from *R. hoffmanni* in that they possess two to five more pairs of subtelocentric chro-

Fig. 17. Karyotypes from a male (AMNH 223185) and female (AMNH 224236) of *Rattus hoffmanni*: 2N = 42, FN = 61 (male) and 62 (female). Pairs 1 and 9 are subtelocentric, and the X-chromosomes are medium-sized subtelocentrics. See text for discussion.

mosomes; *sikkimensis* also has eight instead of seven metacentric pairs (table 3). *Rattus norvegicus, R. exulans, R. losea, R. nitidus, R. argentiventer,* and subspecies of Asian *R. rattus* are most like *R. hoffmanni* in their chromosomal composition. *Rattus norvegicus* and *R. nitidus* have one or two additional subtelocentric pairs compared with *R. hoffmanni*; in some forms of Asian *R. rattus,* pairs 1, 9, and 13 show subtelocentric and

TABLE 3

Summary of Karyotypic Data for *Rattus hoffmanni* and Selected Samples of Other Species of *Rattus*[a]

Species	2N	Autosomes				Sex		FN	Reference
		M	SM	ST	T	X	Y		
Rattus									
norvegicus									
Thailand	42	7	0	4	9	T	T	64	Markvong et al., 1973
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
Malay Peninsula	42	7	0	4	9	T	T	64	Yong, 1969
Calcutta	42	7	0	3	10	T	T	62	Gadi and Sharma, 1983
SE Asia, Oceania	42	7	0	3	10	T	T	62	Yosida, 1973
U.S.S.R.	42	7	0	3	10	T	T	62	Bekasova and Mezhova, 1983
nitidus									
Kathmandu	42	7	0	3	10	T	T	62	Raman and Sharma, 1977
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
turkestanicus									
U.S.S.R.	42	7	0	6	7	ST	T	70	Bekasova and Mezhova, 1983
Afghanistan	42	7	0	7	6	ST	T	71	Niethammer and Martens, 1975
Nepal	42	7	0	4	9	ST	T	65	Niethammer and Martens, 1975
losea									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973; Tsuchiya et al., 1979
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
argentiventer									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973
Vietnam	42	7	0	3	10	T	T	62	Duncan and Van Peenen, 1971
Java	42	7	0	2	11	T	T	60	Yosida et al., 1971
rattus—Asian[b]									
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973
Vietnam, mainland	42	7	0	2	11	T	T	60	Duncan and Van Peenen, 1971
Vietnam, Con Son Is.	42	7	0	2	11	T	T	60	Duncan et al., 1970
Malay Peninsula	42	7	0	2	11	T	T	60	Yong, 1969; Yosida et al., 1971
India	42	7	0	3	10	T	T	62	Raman and Sharma, 1977
SW India	42	7	0	1	12	T	T	58	Lakhotia et al., 1973
Hong Kong	42	7	0	0	13	T	T	56	Yosida et al., 1971
Taiwan	42	7	0	3	10	T	T	62	Yosida et al., 1971
Philippines	42	7	0	3	10	T	T	62	Yosida et al., 1971
rattus rattus[c]									
U.S.S.R	38	9	0	2	7	T	T	60	Bekasova and Mezhova, 1983

TABLE 3—(*Continued*)

Species	2N	Autosomes				Sex		FN	Reference
		M	SM	ST	T	X	Y		
Galapagos Is.	38	9	0	2	7	T	T	60	Patton and Myers, 1974
SW India	38	9	0	2	7	T	T	60	Lakhotia et al., 1973
Australia	38	9	0	2	7	T	T	60	Yosida et al., 1971
rattus—Ceylonese									
Sri Lanka	40	8	0	2	9	T	T	60	Yosida et al., 1972
tiomanicus									
Malay Peninsula	42	7	0	4	9	T	T	64	Yong, 1969
Pulau Tioman	42	7	0	4	9	T	T	64	Yong et al., 1972
P. Perhentian Besar	42	7	0	5	8	T	T	62	Yong et al., 1972
Pulau Tenggol	42	7	0	5	8	T	T	62	Yong et al., 1972
exulans									
Malay Peninsula	42	7	0	2	11	T	T	60	Yong, 1969
Thailand	42	7	0	2	11	T	T	60	Markvong et al., 1973; Tsuchiya et al., 1979
SE Asia, Oceania	42	7	0	2	11	T	T	60	Yosida, 1973
hoffmanni									
Sulawesi	**42**	**7**	**0**	**2**	**11**	**ST**	**T**	**61**—♂ **62**—♀	Present report
everetti									
Philippines	42	7	0	7	6	T	T	70	Tabuena, 1977
sikkimensis									
Thailand	42	8	0	6	6	T	T	70	Markvong et al., 1973
Hong Kong	42	8	0	6	6	T	T	70	Yosida et al., 1971
remotus									
Thailand, Samui I.	42	7	0	4	9	T	T	64	Markvong et al., 1973
annandalei									
Malay Peninsula	42	6	0	3	11	T	T	60	Yong, 1969

[a] The samples of *Rattus* are selected because we list only those taxa that we regard to be species of *Rattus* and only information obtained from specimens we are confident were correctly identified.

[b] Some geographic samples of Asian *R. rattus* have subtelocentric and telocentric polymorphisms in pairs 1, 9, and 13 (see, for example, Yosida et al., 1971; Markvong et al., 1973; Raman and Sharma, 1977; Tsuchiya et al., 1979).

[c] Seven pairs of the metacentric chromosomes range from medium to small; in size and gradation they are closely similar to the seven metacentric pairs in most of the other species of *Rattus*. The other two metacentric pairs are large chromosomes and represent fusion of one pair (*R. rattus* from Sri Lanka) or two pairs (*R. rattus rattus*) of telocentric chromosomes.

TABLE 4

Minimum and Maximum Ambient Air Temperatures (in °F) Recorded from Coastal Lowlands to the Summit of Gunung Nokilalaki in Central Sulawesi[a]

(Elevations are in meters; temperature data are summarized by mean and ranges [in parentheses])

Elev.	Place	Temperature		Number of days	Period
		Minimum	Maximum		
2275	Summit, G. Nokilalaki	51.0 (48–54)	56.6 (52–63)	60	Mar. 4–May 2, 1975
2060	Gunung Nokilalaki	54.7 (51–58)	60.4 (54–65)	60	Mar. 4–May 2, 1975
1730	Gunung Nokilalaki	57.5 (55–60)	64.8 (61–69)	30	Dec. 6, 1973–Jan. 4, 1974
1440	Gunung Kanino	58.4 (52–61)	68.9 (63–76)	32	Jan. 16–Feb. 16, 1975
1150	Sungai Tokararu	61.1 (56–64)	73.9 (69–83)	32	Sept. 12–Oct. 13, 1973
758	Sungai Sadaunta	66.9 (62–70)	75.2 (70–86)	92	Sept. 16–Dec. 16, 1974
290	Sungai Oha Kecil	70.1 (66–73)	78.8 (75–83)	37	July 31–Sept. 5, 1974
136	Sungai Tolewonu	69.8 (67–72)	77.3 (72–81)	57	Jan. 3–Feb. 28, 1976
30	Kuala Navusu	73.6 (72–76)	80.9 (74–87)	95	Aug. 28–Nov. 30, 1975

[a] Each minimum and maximum recording was made during a 24-hour period. Thermometers were placed on or just above the ground beneath the canopy in primary forest. Localities are within the region bounded by the Sungai Miu on the west, Malakosa on the north, Tamadue on the east, and Kulawi on the south. During each period of recordings, rain fell on about half to three-fourths of the days; relative humidities were about 100 percent in early mornings and late evenings, and dropped to the low nineties and high eighties during the middle of each day. Data are from Musser's field notes.

telocentric polymorphisms; the other species are very similar to the Sulawesian rat. The presence of subtelocentric X-chromosomes in *R. hoffmanni* compared with their telocentric counterparts in most of the other species is a notable contrast. The exception is *R. turkestanicus,* in which the X-chromosome is also subtelocentric (table 3). The configuration in *R. turkestanicus,* as well as in *R. hoffmanni,* possibly reflects the addition of heterochromatin to X-chromosomes that would otherwise be telocentric. Results from C-banding would resolve the issue.

Natural History

For 3 years, Musser lived and worked in the forests of central Sulawesi; his field notes provide the information about habitat and habits of *R. hoffmanni* that we summarize below. Our account is sketchy, meant only as an introduction; the natural history of *R. hoffmanni* will be more thoroughly documented in a report being prepared, which will focus on the ecologies of all the native murid rodents found in the central core of the island.

Forest Formations: *Rattus hoffmanni* has either been collected or observed in most forest formations throughout Sulawesi. The species has not been recorded from mangrove associations, but that exception may only reflect the lack of trapping efforts there. Musser obtained samples of the animal from near sea level all the way up to the summit of Gunung Nokilalaki, an altitudinal expanse embracing a wide range of ambient air temperatures (table 4) as well as three primary tropical rainforest formations: lowland evergreen, lower montane, and upper montane. Structure, composition, and other characteristics of each of these formations has been described by Whitmore (1984), and their counterparts on central Sulawesi were sketched by Musser and Dagosto (1987).

Within virgin lowland evergreen forest, most examples of *R. hoffmanni* were caught on the ground and a few in the understory above the forest floor. The species was encountered most frequently in the damp or wet habitats along streams and shaded sides of wet ravines (places similar to those shown in fig. 17 of Musser, 1982b: 27; and in Musser and Dagosto, 1987: 43), areas that remain cool and moist long after the exposed hillsides and ridgetops have lost their wetness to the heat of the day. Protected places in which to move are apparently also important, because most rats were caught beneath good cover and very few in traps set on the open forest floor. The following extracts from

Musser's notes written in the forest provide a few examples of the settings where rats were caught (some of these are pictured in fig. 16 of Musser, 1982b: 26; and figs. 3 and 28 of Musser and Dagosto, 1987: 5, 45).

Kuala Navusu

AMNH 226031 (130 ft): 3 ft above stream on top of rotten trunk forming a bridge from one side of tributary to the other; both banks forested.

AMNH 226041 (700 ft): Damp ground beneath boulder and upturned roots on terrace just above cool and wet ravine; area muddy and densely shrubby.

AMNH 226027 (125 ft): Wet and open ground beneath rotten trunk bridging a stream; trap set on low terrace 5 ft from streambank near where trunk rested on ground; no runway; no undercover near stream, but further back are shrubs and young palms, then dense streamside understory forest shaded by tall, scattered canopy trees.

AMNH 226032 (150 ft): Along streamside among large rocks covered with moss and nearly hidden beneath shrubs, young rattan, and ferns; because of dense cover over rocks and streambanks, area remains wetter longer than nearby hillsides.

AMNH 226040 (500 ft): Caught in runway extending alongside trunk (12 in. diameter) and under upturned roots; treefall sprawls over gently sloping terrace above ponded headwaters of stream; area is shaded by dense undergrowth.

Sungai Tolewonu

AMNH 226493 (450 ft): Wet exposed ground alongside boulder at edge of small, nearly dry tributary stream; trickles connecting shallow pools; streamsides washed and scantily covered with shrubs; no runway or burrow.

Sungai Miu

AMNH 224249 (350 m): Caught on wet, matted leaf litter under dense understory of shrubs, roots, and short trees near treefall that is rotting next to stream.

Sungai Oha Kecil

AMNH 224957 (1100 ft): Wet, rocky, open ground next to stream; no cover.

Sungai Sadaunta

AMNH 224966 (2700 ft): Damp ground beneath splintered base of large, rotten tree lying on terrace above Sungai Sadaunta; covered with moss, small shrubs, ferns, and vines, trunk provides protected spaces and runways along bole and beneath the place it tore and splintered from stump; completely surrounded by dense shrubs (3–4 ft high), tall gingers, and young rattans.

AMNH 224982 (3500 ft): On huge rotten and wet, moss-covered trunk section that is part of jumble of broken pieces of trunk and large limbs laying in steep ravine of tributary stream; treefall and stream overgrown with ferns and shrubs; high forest farther up streamsides; stream courses through and under treefall tangle; area very wet, steep, and shrubby.

AMNH 226825 (3000 ft): Damp ground along base of cut streambank in grove of *Pigafetta* palms on stream terrace; rocky, sandy soil that is always wet; low, dense groundcover of shrubs and smaller plants, understory fig trees common; rotten palm frons litter ground, providing excellent cover.

AMNH 226884 (3000 ft): Beneath large section of trunk covered by dense shrubs, part of a rotting tree fall on stream terrace; damp runways alongside rotting pieces of trunk and large limbs; wide space beneath trunk base where trap had been placed.

In addition to these examples, animals were trapped in other sheltered spots. On the ground beneath the hollow bases of tall living trees, and among the high, sprawling root systems of canopy strangler fig trees were always productive trap sites. Among exposed settings, rotten trunks and limbs, whether smooth or covered with tamped moss, bridging streams and ravines yielded rats more often than others (fig. 18; also, see fig. 18 of Musser, 1982b: 28).

Within primary lower and upper montane rain forests, *R. hoffmanni* was also found adjacent to streams and on the lower sides of ravines, but was encountered just as often on hillsides and ridgetops, probably a reflection of the cooler and wetter forests at higher elevations—especially in upper montane formations (as illustrated in figs. 48–50 of Musser, 1982b: 73–76; and in figs. 1, 26, and 29 of Musser and Dagosto, 1987: 2, 42, 46). Wet, often muddy runways alongside rotting moss-covered trunks and tree limbs (as seen in figs. 51 and 52 of Musser, 1982b: 78, 79) yielded more rats than any other kind of microhabitat. Wet runways beside rocks and along cut banks on steep hillsides were also productive. On the lower ridges and summit of Gunung Nokilalaki, rats were also caught in open, leaf-

Fig. 18. Tropical lowland evergreen rain forest at 100 m near Kuala Navusu, 1975. The spatial configurations formed by ground, understory, and decomposing trees on the ground seen here are common to all forest formations where examples of *R. hoffmanni* were collected. In such places, traps set on the litter-covered forest floor, beneath the rotting trunk and limbs, and on top of the trunk obtained rats. These particular tree limbs projected over a small stream, forming a bridge used by *R. hoffmanni* and other species of rodents.

Fig. 19. Tropical upper montane rain forest at 2242 m on Gunung Nokilalaki, 1975. Here ambient air temperatures are much lower than in lowland rain forest (table 4), the vegetation is nourished by day-long mist and rain, the trees are thin, moss envelops nearly everything, and the canopy is short and the forest less diverse in species than formations at lower altitudes (Musser and Dagosto, 1987). *Rattus hoffmanni* was trapped in runways alongside the moss-covered, wet, and rotting tree trunks and beneath the short bushy cover of rattan rosettes, gingers, and saplings.

Fig. 20. Upper montane rain forest at 2272 m near the summit of Gunung Nokilalaki, 1974. Parts of moss forest are open, the ground wet, and the soil stabilized by clumps of sedges and rotting branches smothered in wet moss. Traps set in these open sites also yielded *Rattus hoffmanni*.

Fig. 21. Transition between upper and lower montane rain forest at 1800 m on ridge-flank of Gunung Nokilalaki, 1973. Traps set beneath these young rattan clusters caught *R. hoffmanni* and other small mammals.

Fig. 22. Lowland evergreen rain forest at 250 ft near Kuala Navusu, 1975. A trap set on a woody vine (¾ inches in diameter) 6 ft above ground (arrow) within the tangle of vines caught *R. hoffmanni*. The forest floor is damp and covered by leaves. Vines are shaded by the dense understory canopy.

Fig. 23. Lowland evergreen rain forest at 350 ft near Kuala Navusu, 1975. Examples of *R. hoffmanni* were trapped on the large woody vine (arrow) arching over a rocky, dry streambed. These twisting pathways provide easy access to understory substrates above the ground.

littered or mossy places on the forest floor, and elsewhere beneath dense cover of rattan rosettes, shrubs, saplings, and gingers (figs. 19–21).

In all forest formations, traps were also set on structures just above the forest floor and high in the understory. Although most *R. hoffmanni* were caught on or near the ground, some were trapped in the understory in the following spots: on top of a large branch 2 ft from ground level, 6 ft above the ground on the trunk of a tree growing out over a stream, in a tangle of woody vines about 6 ft above the leaf-covered floor of the forest, and 8 ft above the ground among the lattice of large aerial roots forming the trunk of a canopy strangler fig. Other successful trap sites are shown in figures 22 and 23.

Musser also found *R. hoffmanni* living where primary forest had been partially cut, where it had been thinned out to accommodate coffee trees, and where it had been removed and was replaced by either scrub or second-growth forest. He never caught the rat in open meadows, agricultural fields, village gardens, or around houses. Even in those habitats resulting from human alteration of primary formations, *R. hoffmanni* was found only in the disturbed formations adjacent to tall forest.

DIET: *Rattus hoffmanni* is a frugivore. Of the 80 stomachs examined to date (representing samples from altitudes between coastal lowlands and mountain summit), a few contained bait, but the rest were full of partially digested fruit pulp. The mass consisted of pulp and fig seeds in most samples. Very small stem and leaf fragments were found with the pulp in others, and insect parts (legs and wings of fruitflies, head and body sclerites of other kinds, and elytra of beetles) were mixed with fruit pulp in a few stomachs. We suspect that the insects (which were all very small and of the kinds attracted to ripe fruit, especially the overripened figs lying on the ground) were inadvertently ingested with the pulp, because the truly insectivorous species of rats use their incisors to snip off legs and wings, eating only the body and sometimes the head (Musser, personal obs.).

Two rats caught in montane forest and one caught in lowlands were kept in cages and fed different foods. The animals from the moss forest ate fruits from a myrtle, *Eugenia* sp.; rattans, *Calamus* spp.; screwpines, *Pandanus* sp.; an understory palm, *Areca vestiaria*; an understory shrub, *Vaccinium* sp.; and an understory fig, *Ficus* sp. The rat caught in lowland forest ate fruits from understory palms, *Pinanga* sp. and *Licuala celebica*; understory figs, *Ficus latimarginata, F. aurita,* and *F. fistulosa*; a canopy-forming strangler fig, *Ficus* sp.; an understory tree, *Madhuca* sp.; and a euphorb canopy tree, *Sapium luzonicum.* Other fruits offered, such as acorns (*Lithocarpus* spp.), were always ignored. Insects, earthworms, or snails given to any of the rats were consistently rejected.

REPRODUCTION: Litters of *R. hoffmanni* contain either four or five young (figures based on counts of embryos). Lactating females with fresh placental scars or small embryos were caught in March, April, May, August, September, October, November, and December at various elevations extending from 125 to 7500 ft (Musser's field notes). This distribution suggests that *R. hoffmanni* breeds throughout the year.

ECTOPARASITES: Sucking lice (*Hoplopleura sembeli*); mesostigmatid, listrophoroid, and anoedid mites; and chiggers (Trombiculidae: *Leptotrombidium deliense, Schoengastia sulawesiensis, Ascoschoengastia indica, Eutrombicula wichmanni, Gahrliepia* sp. X, *Schoutedenichia* sp.), as well as histiostomatid mites (*Histiostoma* sp.) live in the fur of *R. hoffmanni* (Durden, 1986, 1990; Goff and Durden, 1987; Whitaker and Durden, 1987). None of these ectoparasites are restricted to the Sulawesi rat.

MORPHOLOGICAL VARIATION AND ITS TAXONOMIC REFLECTION

Six scientific names have been associated with the *R. hoffmanni* group, either as specific or subspecific designations (Tate, 1936; Laurie and Hill, 1954), implying the presence of demonstrable morphological variation and the significant concordance of that variation with horizontal, altitudinal, and insular distributions. The names *mollicomus* (Miller and Hollister, 1921a) and *palelae* (Miller and Hollister, 1921a) were used to pinpoint morphologically recognizable groups in northern Sulawesi (Ellerman, 1941, 1949; Laurie and

Hill, 1954); *linduensis, subditivus* (Miller and Hollister, 1921a), and *tatei* (Ellerman, 1941) referred to populations in the central core of the island; *mengkoka* (Tate and Archbold, 1935) identified samples from the southeastern arm; and *mollicomulus* (Tate and Archbold, 1935) was applied to specimens from the southwestern peninsula. Two of the names are not based on samples of the *R. hoffmanni* group, as we will elaborate in a following section: *palelae* represents *R. rattus* and *subditivus* is nothing more than *R. nitidus*. In addition, *biformatus* (Sody, 1941), which has never before been tied to *R. hoffmanni,* is available for an insular population of the species.

We tested the strength of the link between scientific name and either a significantly distinctive species of the group or a subunit of a species by comparing means of measurements (tables 5, 6), and qualitative features of the fur, skull (fig. 24), and teeth among samples from the different regions of Sulawesi and from different elevations, and between samples from offshore islands and mainland. The samples are coarse in their composition; each contains males and females and a range in age from young to old adults. Furthermore, sex and age distributions within each sample are uneven: some consist of mostly females or mostly males; some contain primarily young adults, others adults and older animals. A few of the samples are large, others are small; some represent collections from nearby localities and altitudes, others consist of specimens obtained from one site only. In the larger samples, the kinds of data possible to extract are variable. For example, more specimens yielded measurements from appendages and molar rows in the sample from localities 39–44 (table 6) than from cranial measurements because of a high frequency of broken skulls. This unevenness in content did not allow fine resolution of possible patterns of morphological variation within the samples, but did provide sufficient basis for evaluating any possible significant differences among samples from the different regions of Sulawesi.

If there are distinctive limits defined by morphology and geography inherent in most of the populations from which the samples were drawn that are identified by scientific names, we could not detect it in our analyses of the characters we studied. The pattern of chromatic and morphometric variation over northern, middle, and southeastern Sulawesi, as well as offshore islands, does not reflect any clustering correlated with region or island, does not show significant clinal tendencies, and cannot be associated with altitude. By contrast, the few specimens from Gunung Lompobatang in the southwestern arm appear to represent a population that is distinctive in fur coloration and body size. We describe this pattern below in the context of evaluating the characters said to be diagnostic of each of the named forms. First we discuss *mollicomus* from the northern arm, then *linduensis* from central Sulawesi, followed by *mengkoka* of the southeastern peninsula, *biformatus* from Kepulaun Togian, and finally the distinctive *mollicomulus* from Gunung Lompobatang.

Rattus mollicomus was named and described by Miller and Hollister (1921a: 71) based on 13 specimens that were obtained from Gunung Klabat at 5600, 6000, and 6500 ft by H. C. Raven in 1916. Diagnosed as "A member of the *Rattus rattus* group related to *R. hoffmanni,* but with much longer, softer pelage; skull shorter and broader, with spreading zygomata; the antorbital plates less extended forward," Miller and Hollister also noted that "This high mountain species is very different from *Rattus hoffmanni* of the surrounding lowlands. There is no reason to suspect intergradation with *hoffmanni*; and the long, soft pelage and short, broad skull make *R. mollicomus* an easily recognized form." Tate (1936) accepted this diagnosis and included *mollicomus* as a species in his *R. hoffmanni* group, as did Ellerman in 1941. In 1949, however, Ellerman listed *mollicomus* as a subspecies of *R. hoffmanni,* but with a question, an association later repeated by Laurie and Hill (1954).

After comparing the Klabat specimens with samples of *R. hoffmanni* from the lowlands in northern, central, and southeastern Sulawesi, we cannot verify most of the diagnostic cranial features reported by Miller and Hollister. In the series of *mollicomus,* the skull averages slightly, but not significantly, shorter than in the large sample from the lowlands of northeastern and northern Sulawesi (table

TABLE 5

Comparisons of Measurements (in millimeters) among Samples of Adult *Rattus hoffmanni* from Different Regions of Northern Sulawesi

(Mean ± SD, range [in parentheses], and number of specimens are listed for each measurement. Locality numbers key to gazetteer and to map in figure 6.)

	Northeast (localities 1, 9, 14)	Gunung Klabat (locality 6)	Northern (localities 18, 21)	North-central (localities 22, 23)
LHB	170.1 ± 12.08 (144–200) 43	166.3 ± 11.52 (145–187) 12	171.6 ± 12.46 (145–197) 32	172.3 ± 15.63 (142–195) 11
LT	169.5 ± 12.91 (150–192) 42	165.1 ± 13.16 (145–195) 13	178.1 ± 16.00 (155–210) 28	177.4 ± 11.92 (160–192) 10
LHF	38.2 ± 1.44 (35–41) 59	36.8 ± 1.21 (35–40) 13	37.8 ± 1.93 (35–42) 32	38.7 ± 2.05 (36–41) 11
GLS	42.5 ± 1.82 (37.7–46.1) 45	41.0 ± 2.49 (35.7–44.4) 12	42.9 ± 2.13 (38.4–46.2) 32	42.8 ± 2.45 (39.3–45.5) 7
ZB	20.6 ± 0.87 (18.9–22.4) 47	20.0 ± 1.17 (19.1–21.8) 11	20.3 ± 1.07 (18.4–22.2) 28	20.6 ± 1.27 (18.4–21.7) 9
IB	5.9 ± 0.28 (5.3–6.9) 60	5.8 ± 0.21 (5.4–6.1) 13	6.1 ± 0.43 (5.4–7.3) 36	5.9 ± 0.30 (5.3–6.2) 10
LR	13.5 ± 0.77 (11.6–15.3) 60	12.9 ± 1.02 (10.9–14.7) 13	13.6 ± 0.98 (11.6–15.6) 36	13.7 ± 0.84 (12.4–14.7) 11
BR	7.6 ± 0.41 (6.7–8.4) 56	7.2 ± 0.58 (6.2–8.3) 13	7.6 ± 0.52 (6.6–8.6) 36	7.9 ± 0.52 (7.2–8.7) 11
BBC	16.5 ± 0.49 (15.5–17.5) 56	16.2 ± 0.60 (15.0–17.3) 12	16.3 ± 0.61 (15.2–17.5) 32	16.4 ± 0.70 (15.0–17.3) 8
HBC	11.7 ± 0.49 (10.8–13.2) 46	11.7 ± 0.59 (10.5–12.7) 12	11.6 ± 0.37 (10.8–12.4) 31	11.6 ± 0.53 (10.9–12.1) 6
BZP	4.8 ± 0.40 (4.0–5.8) 58	4.5 ± 0.46 (3.5–5.3) 13	5.1 ± 0.48 (4.4–6.1) 36	5.2 ± 0.48 (4.4–5.9) 11
LD	11.1 ± 0.77 (9.3–12.4) 60	10.4 ± 0.89 (8.7–12.0) 13	11.0 ± 1.84 (9.8–12.7) 36	10.9 ± 0.74 (9.5–11.9) 11
PPL	14.0 ± 0.83 (12.2–15.9) 16	13.9 ± 1.06 (12.3–15.7) 9	14.3 ± 0.84 (12.8–15.7) 30	12.8 ± 1.17 (11.6–14.8) 8
LBP	8.4 ± 0.44 (7.0–9.4) 59	8.3 ± 0.56 (7.2–8.8) 13	8.6 ± 0.45 (7.7–9.5) 35	8.6 ± 0.54 (7.5–9.2) 11
BBPM1	3.8 ± 0.40 (3.1–4.5) 44	3.7 ± 0.18 (3.3–3.9) 13	3.8 ± 0.35 (3.1–4.7) 34	3.8 ± 0.30 (3.3–4.2) 10
LIF	8.0 ± 0.52 (6.9–9.3) 60	7.9 ± 0.45 (7.1–8.5) 13	8.1 ± 0.59 (7.1–9.5) 35	7.8 ± 0.55 (7.0–8.9) 11
BIF	2.8 ± 0.27 (2.0–3.6) 60	2.6 ± 0.28 (2.1–3.1) 13	2.7 ± 0.46 (2.4–3.3) 34	2.7 ± 0.27 (2.2–3.2) 11
LB	6.9 ± 0.40 (6.0–7.7) 54	7.1 ± 0.35 (6.4–7.2) 12	7.2 ± 0.41 (6.1–7.9) 33	7.2 ± 0.42 (6.6–7.8) 10
CLM1–3	7.3 ± 0.34 (6.4–7.7) 24	7.7 ± 0.38 (7.0–8.2) 11	7.3 ± 0.25 (6.5–7.8) 36	7.3 ± 0.34 (6.7–7.9) 12
BM1	2.4 ± 0.12 (2.1–2.6) 59	2.4 ± 0.14 (2.1–2.6) 13	2.2 ± 0.48 (2.2–2.4) 34	2.3 ± 0.09 (2.1–2.4) 11

TABLE 6

Comparisons of Measurements (in millimeters) among Samples of Adult *Rattus hoffmanni* from the Central Core of Sulawesi, Its Southeastern Arm, and the Togian Islands

(Mean ± SD, range [in parentheses], and number of specimens are listed for each measurement. Locality numbers key to gazetteer and to map in figure 6.)

	Central (localities 39–44)	Southeastern (localities 91–93)	Kepulauan Togian (locality 99)
LHB	185.1 ± 9.78 (167–211) 35	177.8 ± 6.30 (172–186) 5	190.3 ± 12.13 (175–208) 12
LT	174.3 ± 10.32 (155–200) 35	171.8 ± 13.86 (150–186) 5	164.2 ± 10.56 (147–183) 12
LHF	38.3 ± 5.50 (36–42) 35	39.2 ± 0.84 (38–40) 5	38.3 ± 1.49 (36–41) 12
GLS	42.7 ± 1.40 (40.2–45.7) 21	43.4 ± 1.25 (42.6–44.9) 3	42.7 ± 2.25 (39.6–47.6) 12
ZB	21.1 ± 0.61 (19.7–22.3) 23	21.1 ± 0.87 (20.4–22.1) 3	20.3 ± 1.22 (18.9–22.5) 12
IB	6.0 ± 0.27 (5.3–6.6) 33	6.2 ± 0.23 (6.1–6.5) 3	6.3 ± 0.31 (5.7–6.7) 12
LR	13.8 ± 0.86 (12.0–16.2) 33	13.5 ± 0.29 (13.1–13.7) 4	14.0 ± 1.10 (12.8–16.8) 12
BR	7.7 ± 0.46 (7.0–8.9) 34	8.2 ± 0.26 (7.8–8.4) 4	8.2 ± 0.43 (7.6–9.0) 12
BBC	16.6 ± 0.41 (15.7–17.4) 23	17.0 ± 0.50 (16.5–17.6) 4	16.5 ± 0.56 (15.5–17.2) 12
HBC	11.6 ± 0.77 (11.0–12.6) 26	11.7 ± 0.61 (11.0–12.1) 3	11.4 ± 0.43 (10.7–12.0) 12
BZP	4.9 ± 0.40 (4.1–5.8) 35	5.3 ± 0.56 (4.7–6.0) 4	5.2 ± 0.38 (4.5–5.7) 12
LD	10.9 ± 1.86 (10.1–12.7) 33	10.8 ± 0.72 (10.2–11.5) 4	11.2 ± 0.80 (10.0–12.8) 12
PPL	14.1 ± 0.63 (13.3–15.6) 22	14.9 ± 0.78 (14.3–15.4) 2	13.7 ± 0.67 (12.8–15.2) 11
LBP	8.6 ± 0.43 (7.7–9.1) 34	8.8 ± 0.41 (8.3–9.3) 4	8.6 ± 0.37 (7.9–9.1) 12
BBPM1	3.7 ± 0.70 (3.3–4.2) 31	4.1 ± 0.05 (4.1–4.2) 4	3.9 ± 0.46 (3.2–4.8) 12
LIF	8.0 ± 0.48 (7.1–9.1) 35	8.0 ± 0.10 (7.9–8.1) 4	7.6 ± 0.66 (6.8–9.2) 12
BIF	2.5 ± 0.46 (2.0–3.2) 33	2.8 ± 0.22 (2.6–3.1) 4	3.0 ± 0.34 (2.7–3.7) 12
LB	6.9 ± 0.24 (6.5–7.5) 32	7.4 ± 0.18 (7.2–7.6) 4	6.9 ± 0.20 (6.6–7.3) 12
CLM1–3	7.3 ± 0.23 (6.7–7.7) 34	7.4 ± 0.30 (6.9–8.0) 7	7.0 ± 0.12 (6.8–7.1) 14
BM1	2.1 ± 0.60 (2.1–2.5) 33	2.3 ± 0.05 (2.3–2.4) 4	2.2 ± 0.05 (2.1–2.3) 12

5). Mean differences in the zygomatic breadth—a measure of the "spreading zygomata"—between the sample of *R. mollicomus* and those from northern lowlands are also slight and insignificant. No significant differences exist between the highland sample and those from the lowlands in mean values of interorbital, rostral, or braincase breadths, all dimensions that provide an estimate of a "broad skull." Furthermore, we did not find any important distinctions between the samples in general configuration of the cranium, including breadth of the zygomatic plate and depth of the zygomatic notch (the latter is a measure of the forward extension of the "antorbital plates"); in mean values from other cranial and dental measurements; or in lengths of head and body, tail, and hind feet.

The pelage of *mollicomus* is slightly longer and somewhat softer to the touch than is the fur on most specimens from the lowlands, but it is indistinguishable from examples of *R. hoffmanni* taken on mountains elsewhere in Sulawesi. Our comparisons of samples from low altitudes with those from higher places along transects in both central and southeastern Sulawesi reveal that while the variation in dimensions and qualitative cranial and dental characters is apparently not correlated with altitude (table 7), fur texture is: animals living in cool, moss forest tend to have slightly longer and softer fur than do those inhabiting warmer forests at lower elevations. Differences in this aspect of the pelage between samples from Gunung Klabat and those from lowlands in the northeast likely reflect a phenotypic response to ambient environmental factors. However, it does not reflect a genetic distinction great enough to suggest the presence of two species, as Miller and Hollister claimed.

We could not detect any consistent contrasts in fur color between the sample of *mollicomus* and those from lower elevations in the northeastern and northern arm. The range of variation in tone characterizing both dorsal and ventral coats, as well as the range in amount of buff throughout the underparts, overlaps greatly between highland and lowland series. Except possibly the sample from the southwestern arm of the island, we could not identify any group of specimens that could consistently be recognized as distinct by chromatic features. Subtle differences in tone can be seen among some of the smaller samples, but that range is encompassed within larger samples obtained from a single locality; chromatic differences were also clearly not concordant with altitude.

The name *mollicomus* identifies only a group of specimens caught in mountain forest in northeastern Sulawesi. We have no evidence that suggests that the sample represents any entity other than *R. hoffmanni*. *Rattus mollicomus* Miller and Hollister, 1921, therefore should be regarded as a subjective synonym of *R. hoffmanni*.

Ranges of variation of features associated with skins, skulls, and dentitions in samples at hand from the northern arm of Sulawesi appreciably overlap the range of variation we observe in samples obtained from the central region of the island. The presence of a population in central Sulawesi that is set apart by distinctive phenotype from populations occurring elsewhere on Sulawesi is not indicated by our observations; such an entity, however, has been recognized in the taxonomic literature under the subspecific title *linduensis*.

Rattus hoffmanni linduensis is another Miller and Hollister (1921a: 70) combination, a name based on 49 specimens collected by Raven from Tomado, Bumbarjaba, Kulawi, Gunung Lehio, Pinedapa, and Rano Rano (see gazetteer and fig. 6). All localities are from highlands (500–2200 m) in central Sulawesi. Miller and Hollister diagnosed *linduensis* as being like *Rattus hoffmanni* of northern Sulawesi, "but averaging smaller and darker; with longer, softer pelage; and smaller skull." They also remarked that "All of these specimens of *Rattus hoffmanni* from the highlands of Middle Celebes are readily separable from specimens of the typical form from North Celebes by the long, soft, richly colored pelage. The underparts average darker also, more grayish buff; the skulls average distinctly smaller, but the teeth are large, as in the typical form." In 1941, Sody (p. 315) reinforced Miller and Hollister's opinion of the distinctness of *linduensis* when he reported on eight specimens in the collection at Bogor, Indonesia, indicating that his material was "smaller and more warmly colored than *hoffmanni* typicus." Later, Musser

(1971) showed *R. tatei,* named and described by Ellerman in 1941 from specimens obtained by Frost in central Sulawesi, to be a synonym of *R. h. linduensis,* and thought the latter to represent a recognizable population of *R. hoffmanni.*

Now that we have studied additional material of *R. hoffmanni* from localities throughout most of Sulawesi, we cannot verify the distinctions between *R. h. linduensis* and *R. h. hoffmanni* that Miller and Hollister thought were diagnostic. Differences between samples from northern and central Sulawesi in mean values of most dimensions are slight (tables 5, 6) and not significant. Specimens of comparable age from each region and similar elevation, when compared side by side, are indistinguishable from one another in external characteristics; dental features; and cranial proportions, dimensions, and conformation. We also do not appreciate the differences in color and texture of pelage reported by Miller and Hollister; both dark and paler fur can be found within the same sample in our material. A difference in fur texture does exist if rats from high elevations are compared with those caught in lowlands, as we previously noted. A similar contrast marks the variation in texture of pelage along a transect from lowlands to mountaintop in central Sulawesi, and we cannot find evidence in other characters indicating that more than one species of the *R. hoffmanni* group inhabits such an altitudinal range in the central core of the island.

We were able to examine sufficient material collected from different elevations to test any possible correspondence between altitude and phenotypic variation. We have already discussed fur qualities. If length of cranium is used as a rough estimate of body size, mean values from samples at higher elevations (about 1000 m and above) are slightly smaller than those from lowland samples (table 7). In this case, however, the lowland series contain mostly adult and old adult rats, which shift the average to the high side, whereas the highland samples contain a higher percentage of young adult animals. Length of maxillary toothrow is not influenced by age in the young to old adult categories, and forms larger samples because this length can be measured in broken crania that disallow measuring greatest length of the skull. Our analysis shows that toothrow length is not related to altitude (table 7). Along the transect from which our series were collected, there is a slight but not statistically significant trend from short molar rows at low elevations to longer rows at higher sites. In these and other characteristics, we cannot identify any significant breaks between samples along an altitudinal transect in central Sulawesi or horizontally between there and the northern arm that would suggest more than one species, or recognizable subunits of a single species. Based on observations of the morphology characterizing samples available to us, we consider *R. h. linduensis* Miller and Hollister, 1921, along with *R. tatei* Ellerman, 1941 (see Musser, 1971), to be subjective synonyms of *R. hoffmanni.*

In 1935, Tate and Archbold (p. 3) named and described *Rattus hoffmanni mengkoka* from specimens obtained by Gerd Heinrich in southeastern Sulawesi during January 1932. His collections were made in three areas: Wawo, on the coastal plain of the Gulf Van Bone, at an elevation of 50 m and west of Pegunungan Mekongga; Gunung Masembo, 550 m, on the southeastern slopes of Pegunungan Mekongga; and two camps on Gunung Tanke Salokko, northwest of Gunung Masembo at 1500 and 2000 m on the eastern slopes of Pegunungan Mekongga (fig. 6). Heinrich obtained specimens of *Rattus hoffmanni* from each of these localities.

Tate and Archbold gave only a brief description of *R. h. mengkoka* and apparently relied on the literature for comparative data from other previously described subspecies of *R. hoffmanni.* They stated that specimens from the lowlands were similar to those from the highest places, gave a brief and undiagnostic description of the pelage ("rather long, harsh and thin, the hairs as with most members of the group, fuscous, tipped with ochraceous tawny; under parts grayish white, i.e., bases gray, tips dirty white. Fine hairs of hands and feet dirty white. Tail entirely fuscous"), provided measurements of the holotype (AMNH 101062), and stated that the skull of *R. h. mengkoka* approximated Hoffmann's (1887) measurements and drawing of the holotype of "*Mus rattus celebensis*" (= *R. h. hoffmanni*) but differed in having a nar-

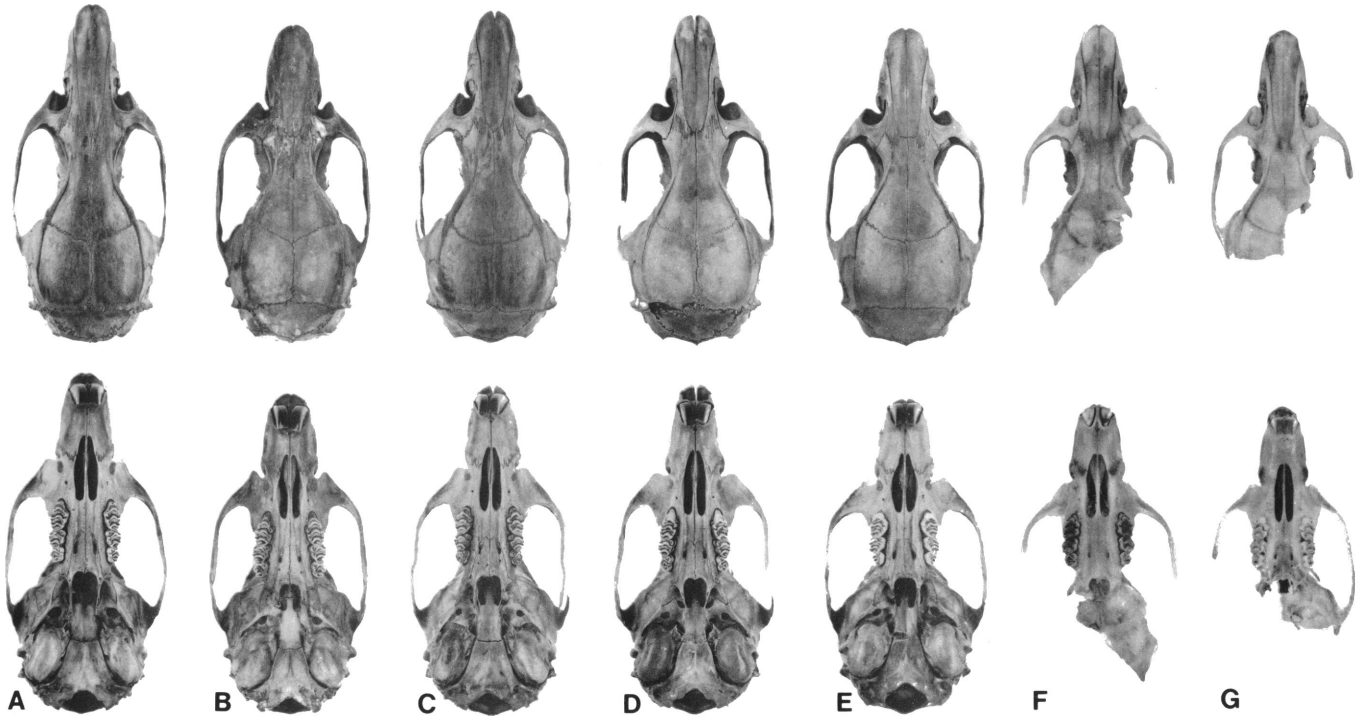


Fig. 24. Comparisons among crania (×1) of adult *Rattus hoffmanni* (**A-F**), representing samples from different regions of Sulawesi, and *R. mollicomulus* (**G**) from Gunung Lompobatang. **A.** Lowland *hoffmanni* from the northeastern arm (USNM 216833). **B.** The mountain sample from Gunung Klabat described as *mollicomus* (USNM 217758). **C.** The central Sulawesian *linduensis* (USNM 219583). **D.** *mengkoka* from the southeastern peninsula (AMNH 101066). **E.** The sample of *biformatus* from Pulau Malenge in the Togian Islands (AMNH 153352). **F.** The lowland sample of *hoffmanni* from Bantimurung near the tip of the southwestern arm (AMNH 101290). **G.** *R. mollicomulus* from Gunung Lompobatang (AMNH 101134, the holotype). See discussion in text.

TABLE 7

Measurements (in millimeters) of Cranium (Adults) and Toothrow (All Ages) Lengths Compared among Samples of *Rattus hoffmanni* Collected at Elevations (in meters) along a Transect Extending from near Sea Level to Mountain Summit in Central Sulawesi[a]

Site	Elevation	Greatest length of skull	Crown length of M1–3
Gunung Nokilalaki	1730–2270	**41.01** ± 1.25 (39.1–43.4) 13	**7.40** ± 0.21 (7.0–7.8) 41
P		0.2–0.1	>0.9
Gunung Kanino	1300–1600	**42.00** ± 1.19 (40.5–43.5) 5	**7.39** ± 0.26 (6.7–7.7) 29
P		0.4–0.3	0.6–0.5
Sungai Tokararu	1150–1256	**42.60** ± 1.27 (40.6–44.3) 6	**7.47** ± 0.23 (7.0–7.8) 29
P		0.9–0.8	0.1–0.05
Sungai Sadaunta	600–1060	**42.65** ± 1.40 (40.2–45.7) 21	**7.24** ± 0.24 (6.7–7.7) 38
P		0.2–0.1	>0.9
Sungai Miu	290–455	**43.57** ± 1.43 (41.9–46.1) 11	**7.25** ± 0.35 (6.7–7.7) 15
P		0.9–0.8	0.5–0.4
Kuala Navusu–Sungai Tolewonu	30–212	**43.68** ± 1.35 (41.1–45.5) 8	**7.10** ± 0.28 (6.6–7.5) 14

[a] Mean ± SD, range (in parentheses), and number of specimens are listed for each measurement. *P* is the significance probability derived from a table of cumulative Student's *t* distribution; values less than 0.01 were considered significant enough to reject the hypothesis that means of any two samples were drawn from the same population. Sites of collections are listed in gazetteer and mapped in figure 6.

rower zygomatic plate and a shorter toothrow.

Five of the eight specimens are adults, but only four are complete enough to measure. In color and texture of pelage, body size, and cranial configuration and dimensions, specimens of *mengkoka* are closely similar to specimens of comparable age in samples from central and northern Sulawesi. Zygomatic plates of *mengkoka* are not narrower, as Tate and Archbold claimed, and the toothrows are not shorter (tables 5, 6).

The samples from southeastern Celebes represent a population of *R. hoffmanni* that in morphology of skins and skulls does not differ importantly from samples collected in central and northern Sulawesi. *Rattus h. mengkoka* Tate and Archbold, 1935, should be considered a subjective synonym of *R. hoffmanni,* a conclusion implied in 1941 by Sody (p. 315) when he reported on the two specimens from Pegunungan Mekongga that are housed in the Museum Zoologicum Bogoriense at Bogor, and pointed out that the cranial characters used by Tate and Archbold to distinguish *mengkoka* were not diagnostic.

Very little information exists on the kinds of morphological variation in samples from islands off the coast of Sulawesi compared with that observed in series from the mainland. Only two islands have yielded collections. One specimen comes from Pulau Lembeh (locality 7), close off the eastern margin of the northeastern arm; in characteristics associated with skin and skull it is inseparable from specimens of comparable age collected on the adjacent mainland. A larger sample was obtained on Pulau Malenge (locality 99; fig. 6) in the Togian Archipelago.

Rattus biformatus has been applied to the sample from Pulau Malenge. Sody (1941) described two species based on collections from that island. One was *Rattus sapoensis* (p. 306), which is not a distinctive species but an insular population of the house rat, *R. rattus* (Musser, 1977). The other Sody described as *R. biformatus* (pp. 306–307), writing that

> After separating *R. sapoensis,* there remain (besides 1 *R. rattus*) 7 other rats from Malengi, also superficially much resembling *R. rattus,* but short tailed like *sapoensis.* They differ from *sapoensis* by not possessing such strongly elongated piles, their larger teeth (breadth of m^1 2.0–2.2 mm, against 1.85 in the type of *sapoensis*), somewhat greater palatal length, zygomatic and rostral breadths. However, the 7 rats between them show much variation, even two mammae formulae!

As regards the colour of the belly they do not belong to one close systematic unit, but I am unable to find any further characters, changing correspondingly to the belly colour and I therefore keep them together.

The type plus the 3 other ones of the same group (type a) are well densely haired (compacter and longer than *R. rattus*). Fur of dorsal side consisting of woolly hairs (dark grey with ochraceous buff tips), few hard spines (whitish with black tips), intermixed with rather elongated bristles (black, sometimes light tipped at the sides). Belly with soft grey hairs, between which many harder ones with long light grey (whitish) tips. Chest buffy, middle line of chest and belly slightly darker, chin lighter. The type shows on head and chest some white hairs placed together. Tail black, + 9 rings per cm. Mammae in type and second ♀ 2 + 3 = 10.

The other specimens (type b) are strongly suffused with buff or ochraceous buff over the whole ventral side. One of the ♀♀: 2 + 3 = 10, the other: 1 + 3 = 8.

The entire sample of *biformatus* consists of examples of *R. hoffmanni,* which is reflected by their short guard hairs ("piles") and wide teeth, primary features Sody used to distinguish *biformatus* from *sapoensis,* and two among several of the characteristics that separate examples of house rats from those of *R. hoffmanni.* Although insular in distribution, morphology of the specimens in the sample we have studied is so similar to characteristics of specimens from mainland Sulawesi (tables 5, 6) that we treat *Rattus biformatus* Sody, 1941, as another subjective synonym of *R. hoffmanni.* There are only three characters we could find in the Malenge sample that might indicate some morphological divergence from mainland populations. The molar row of the island series is shorter ($P = 0.05$–0.02, Malenge versus central Sulawesi) than any other sample except the one from the southwest peninsula; the incisive foramina are broader ($P = 0.02$–0.01, Malenge versus central Sulawesi), a contrast shown in figure 24. Out of the six females in the Malenge sample, four have four pairs of mammae, the usual condition in *R. hoffmanni* (in which a pectoral pair is absent), but two (one of them the holotype) have a pectoral pair. In each specimen, however, the pectoral teats are minute compared with the large and fully developed nipples on the rest of the body and were probably not functional when the rats were alive. Rarely have we encountered this kind of variation in any sample from the mainland of Sulawesi.

Finally we come to the meager samples representing all we know about morphological variation and altitudinal distribution of the *R. hoffmanni* group in the southwestern peninsula of Sulawesi. Two series are available for study. One consists of six specimens collected below 100 m on the western coastal plain at Tempe (locality 95) and Bantimurung (locality 96); only three of these are adults and their skulls are in fragments. In color and texture of fur, size of body, and absolute lengths and proportions of appendages, the specimens are inseparable from those in samples of *R. hoffmanni* obtained from lowland habitats in the southeastern peninsula of Sulawesi, its central core, and northern arm (compare table 9 with tables 5, 6). The larger pieces from the adult crania closely resemble specimens of *R. hoffmanni* in the other lowland samples in actual measurements of some dimensions, proportions, and overall cranial conformation (table 9; figs. 24, 25). These two samples from the southwestern plains, although small in number of specimens and unsatisfactory in quality of preservation, indicate that the population of *R. hoffmanni* inhabiting the coastal lowlands on the southwestern arm is very similar in chromatic and textural features of pelage and morphology of external, cranial, and dental elements to populations of the species that occur at low elevations throughout other regions of Sulawesi.

Rattus hoffmanni is also represented in the lowlands of southwestern Sulawesi by two subfossil fragments. A partial dentary with a complete toothrow was collected at Batu Ejaya (locality 98) from sediments less than 1000 years Before Present (Musser, 1984). The other is an edentulous piece of right dentary obtained from Trench A in Leang Burung 1 (as opposed to Leang Burung 2; see Glover, 1981) (locality 97). The time tied to this piece is associated with charcoal dated "2820 ± 210 B.P." (Mulvaney and Soejono, 1970: 171). The specimen from Batu Ejaya was originally identified as *R. hoffmanni* and referred to *R. h. mollicomulus,* but it and the fragment from Leang Burung 1 match the series from Bantimurung in size of teeth and length of toothrow alveolus (table 8)—they are a sample of lowland *R. hoffmanni* and not mountain *R. mollicomulus.*

TABLE 8

Measurements (in millimeters) of Right Lower Molars and Alveolar Rows from Recent and Subfossil Samples of the *Rattus hoffmanni* Group from Southwestern Sulawesi

Species and locality	bm1	bm2	bm3	clm1–3	alm1–3
R. mollicomulus					
Gunung Lompobatang					
AMNH 101134	1.7	1.9	1.7	6.7	6.8
AMNH 101191	1.7	1.9	1.6	6.4	6.7
AMNH 100995	1.8	2.0	1.7	6.7	6.7
R. hoffmanni					
Bantimurung					
AMNH 101290	1.8	1.9	1.7	6.8	6.7
AMNH 101291	1.8	2.0	1.7	6.8	6.8
AMNH 101292	2.0	2.1	1.8	6.9	6.9
Batu Ejaya					
Specimen 35	1.9	2.1	1.7	6.9	7.0
Leang Burung 1					
AMNH 265045	—	—	—	—	7.0[a]

[a] An estimate; the posterior margin is missing.

Rattus mollicomulus Tate and Archbold

Rattus mollicomulus Tate and Archbold, 1935: 4 (type locality, Wawokaraeng, Gunung Lompobatang, 1500 m, southwestern Sulawesi; holotype AMNH 101134).

The other sample from the southwestern peninsula contains five rats collected at 1100 m from Lombasang (locality 100), just northwest of Gunung Lompobatang, and at 2000 m on Gunung Lompobatang itself (locality 101). Only two of the five are adults; unfortunately, their skulls are broken and some of the pieces have been lost. This material, preserved as stuffed museum skins and associated skulls, is not a sample of *R. hoffmanni.* Three of the specimens were the basis for Tate and Archbold's description of the new species, *Rattus mollicomulus,* which they characterized (1935: 4) as a "member of the *hoffmanni* group but of quite small size, the long soft pelage indicating that it inhabits the highlands." Not only is the fur of *mollicomulus* long and soft compared with that of specimens in the samples from the coastal plain in which the pelage is short and coarse, but it is also paler: upperparts are pale yellowish brown and underparts are silvery white tinged here and there with buff; dorsal surfaces of the hind feet are whitish rather than brown. In addition to this difference in texture and tone of pelage, specimens of *mollicomulus* are much smaller than those of comparable age in the series from Bantimurung, and they are smaller than rats in any other sample of *R. hoffmanni* we examined, no matter what region of Sulawesi or what altitude the samples came from (table 9).

The contrast in body size is evident from the crania illustrated in figure 25 and the measurements compared in table 9. There, dimensions of two adult *mollicomulus* from Wawokaraeng on Gunung Lompobatang are compared with those of three specimens of *R. hoffmanni* of comparable age from Bantimurung; a series from Gunung Kanino at 1400–1600 m collected in the mountains of central Sulawesi; and a sample from Kuala Navusu, below 300 m near the coast. Three important observations are to be extracted from the table. First, series from Gunung Kanino and Kuala Navusu are closely similar to one another and do not show significant average differences in measurements, a pattern we described previously when we demonstrated that size in *R. hoffmanni* does not vary appreciably with altitude in either the central part or northeastern arm of Sulawesi (table 7). Second, specimens from Bantimurung on the coastal plain northwest of Gunung Lompobatang resemble rats from Kuala Navusu and Gunung Kanino in av-

erage values, but not the individuals of *mollicomulus*. Finally, the two adults from Gunung Lompobatang (Wawokaraeng) are much smaller than specimens of similar age in the sample collected at a comparable altitude on Gunung Kanino and equally smaller than the adults obtained on the nearby coastal plain at Bantimurung.

We assume our samples from the southwestern arm of Sulawesi reliably index the contrast in morphologies between lowland and mountain populations there. If so, that pattern of variation is discordant with the picture we have observed in other regions of the island—slight or no significant change in most characteristics associated with skins and skulls along an altitudinal gradient. Attributes of the series from the southwest suggest an insignificant amount or cessation of gene flow between the population on Gunung Lompobatang and the one at lower altitudes. A comparable disjunction is not reflected in features of the samples from elsewhere on Sulawesi, where material has been collected at different altitudes ranging from near sea level to mountain summit. The information gleaned from our samples, small as they may be, strongly suggests that the highland form has had a different evolutionary history from the lowland population, an entity whose antecedents are inseparable from the evolutionary history of *R. hoffmanni* in general. We hypothesize that the specimens at hand from about 1100 to 2000 m on the foothills and upper slopes of Gunung Lompobatang represent a distinct species, *Rattus mollicomulus* Tate and Archbold, 1935. This hypothesis can be tested by determining the morphological and ecological characteristics of not only larger samples collected at both high and low altitudes, but also series obtained at intermediate elevations. Our view reinforces the original characterization, Tate's (1936) inclusion of *mollicomulus* as another species in his *R. hoffmanni* group, and Sody's (1941) recognition of it as a species related to *R. hoffmanni*, but not Ellerman's (1949) or Laurie and Hill's (1954) arrangement of *mollicomulus* as a questioned subspecies of *R. hoffmanni*.

The discontinuity in morphology that appears to be related to altitude in the Gunung Lompobatung region is not an isolated pattern peculiar to only members of the *R. hoffmanni* group, but is common to yet another species pair in *Rattus* and pairs in the genera *Bunomys* and *Paruromys* (table 10). In each couple, one species is found on Gunung Lompobatang and nowhere else, and the other is known only by samples from the coastal lowlands. The highland species are represented by skins and skulls, and their diagnostic morphology is contained in characters of the fur, appendages, skull, and dentition. Samples of two of the lowland species contain skins and skulls as well as subfossil fragments (Musser, 1984); characters of the other three are those observed in subfossil pieces only (Musser, unpubl.). In each set, the phylogenetic relationship between mountain and plains entities appears to be that of sister species.

This biogeographic pattern may reflect the pulses of mountain building and cyclic isolation of the southwestern peninsula of Sulawesi as an island. Gunung Lompobatang consists of Miocene, Pliocene, and Quaternary volcanic sediments; during the late Miocene and early Pliocene, most of western Sulawesi was beneath the sea, and Gunung Lompobatang may have been an island (Audley-Charles, 1981). Later, during Pleistocene times, the southwest arm was part of an ancient Sulawesi archipelago (Fooden, 1969). Interactions between time and tectonics may have had a profound influence on evolution of both extinct and extant mammalian faunas (Musser, 1987).

Comparisons with Nonendemic *Rattus*

Determining the morphological and distributional limits of *R. hoffmanni* requires not only observation and description of the samples we have identified as that taxon, but also comparisons between those samples and specimens representing other species of *Rattus* that are known to occur on Sulawesi. The five that require contrast with *R. hoffmanni* are *R. rattus, R. nitidus, R. exulans, R. argentiventer,* and *R. norvegicus*. The morphological features characterizing *R. hoffmanni* have been considered by some workers to closely resemble characters of these other species. To Ellerman (1949: 190), for example, *R. hoffmanni* was "probably a local race of *R. rattus* in which a pair of mammae

TABLE 9

Comparisons of Measurments (in millimeters) between Samples of *Rattus hoffmanni* and *Rattus mollicomulus*

(Mean ± SD, range [in parentheses], and number of specimens are listed for each measurement. Locality numbers key to gazetteer and to map in figure 6.)

		Southwestern Sulawesi					
	Central Sulawesi: *R. hoffmanni* **Kuala Navusu** 38–212 m (locality 71)	*R. hoffmanni* **Bantimurung** 0–100 m (locality 96)			*R. mollicomulus* **Gunung Lompobatang** 1500 m (locality 101)		Central Sulawesi: *R. hoffmanni* **Gunung Kanino** 1400–1600 m (localities 58–62)
		AMNH 101289	AMNH 101290	AMNH 101292	AMNH 101134[a]	AMNH 101191	
Age	Old ad.–Adult	Old ad.	Adult	Adult	Adult	Adult	Old ad.–adult
LHB	189.8 ± 6.18 (179–200) 8	180	175	170	153	157	182.8 ± 7.69 (172–194) 12
LT	174.0 ± 7.09 (166–183) 8	166	160	157	141	154	173.7 ± 10.60 (156–187) 12
LHF	39.6 ± 1.51 (38–42) 8	38	37	37	33	35	39.7 ± 1.61 (37–42) 12
IB	5.8 ± 0.23 (5.4–6.0) 8	6.2	5.7	—	5.4	5.4	6.0 ± 0.19 (5.7–6.3) 11
LR	14.3 ± 0.32 (13.7–14.8) 8	14.2	13.3	—	12.4	—	13.8 ± 0.64 (12.8–15.0) 11
BR	7.9 ± 0.25 (7.5–8.3) 8	8.4	7.6	—	6.6	—	7.6 ± 0.41 (6.8–8.3) 11
BBC	16.4 ± 0.21 (16.1–16.7) 7	—	—	15.9	—	15.4	16.5 ± 0.13 (16.3–16.6) 4
HBC	11.7 ± 0.98 (11.4–11.8) 7	—	—	11.4	—	—	12.1 ± 0.32 (11.6–12.3) 4
BZP	5.1 ± 0.28 (4.7–5.5) 8	5.7	4.9	4.7	4.2	—	4.9 ± 0.27 (4.5–5.3) 11
LD	11.5 ± 0.28 (11.1–12.0) 8	12.1	11.4	11.0	10.6	—	10.8 ± 0.55 (10.0–11.9) 11
LBP	8.8 ± 0.27 (8.5–9.2) 8	8.2	8.0	—	7.5	—	8.6 ± 0.42 (7.9–9.2) 12
BBPM1	4.2 ± 0.17 (4.0–4.4) 8	4.6	4.5	—	3.7	—	4.1 ± 0.31 (3.5–4.5) 12
LIF	8.0 ± 0.42 (7.6–8.8) 8	8.2	8.4	7.3	7.5	—	7.8 ± 0.40 (7.0–8.3) 11
BIF	2.7 ± 0.19 (2.5–3.1) 8	2.9	3.1	—	2.4	—	2.6 ± 0.17 (2.4–2.9) 11
LB	7.2 ± 0.17 (6.9–7.3) 8	7.7	7.6	7.0	6.4	6.7	7.0 ± 0.19 (6.6–7.3) 11
CLM1–3	7.1 ± 0.34 (6.6–7.5) 8	6.8	6.8	6.8	6.6	—	7.4 ± 0.31 (6.7–7.7) 12
BM1	2.2 ± 0.09 (2.1–2.3) 8	2.2	2.2	2.2	2.1	—	2.2 ± 0.10 (2.1–2.4) 12

[a] The holotype of *Rattus mollicomulus* Tate and Archbold, 1935.

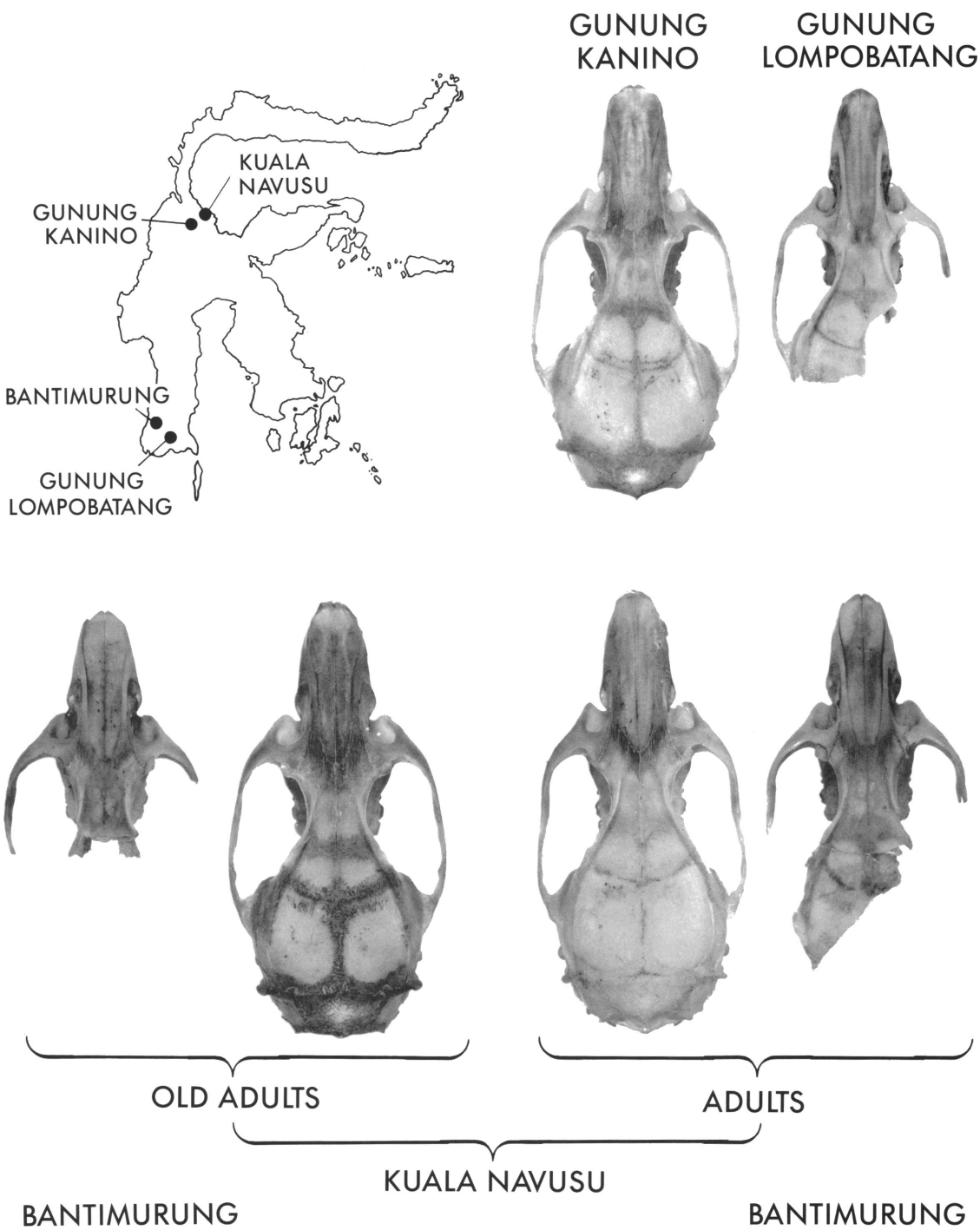


Fig. 25. Comparisons of crania (×1.5) between samples of *Rattus hoffmanni* and *R. mollicomulus*. In the bottom row, an old adult (AMNH 226026) and adult (AMNH 226033) from coastal lowlands of central Sulawesi near Kuala Navusu are compared with an old adult (far left; AMNH 101289) and adult (far right; AMNH 101290) from Bantimurung on the coastal plain near the southwestern tip of Sulawesi to illustrate the close correspondence in size between these samples of lowland *R. hoffmanni*. In the top

TABLE 10
Altitudinal Distributions of the Species-Pairs in *Rattus, Bunomys,* and *Paruromys* That Occur in the Southwestern Peninsula of Sulawesi[a]

Endemic to upper slopes of Gunung Lompobatang	Counterpart in adjacent lowlands	Occurrence elsewhere
Rattus mollicomulus	*Rattus hoffmanni*	Throughout Sulawesi[b]
Rattus bontanus	*Rattus foramineus*	Southwestern arm only[b]
Bunomys heinrichi	*Bunomys* sp. A	Central Sulawesi[c]
Bunomys coelestis	*Bunomys chrysocomus*	Throughout Sulawesi[c]
Paruromys ursinus	*Paruromys dominator*	Throughout Sulawesi[c]

[a] This summary is based on samples of skins and skulls as well as subfossil material documented in publications (Musser, 1984, 1987) and manuscripts being prepared (Musser, unpubl.; Musser and Holden, unpubl.).

[b] Samples contain museum skins with accompanying skulls in addition to subfossil pieces (Musser, 1984).

[c] That part of the range in the southwestern peninsula is documented by subfossils; elsewhere in Sulawesi it is based on skins and skulls (Musser, unpubl.).

have become suppressed." Furthermore, specimens of *R. hoffmanni* are frequently misidentified, either in the taxonomic literature or in collections in museums, as either *R. rattus, R. nitidus,* or *R. exulans*; conversely, specimens of those species have been incorrectly described or identified as examples of *R. hoffmanni.* Here we focus on the distinctions separating samples of those three species from series of *R. hoffmanni*; as far as we know, that Sulawesian endemic has never been confused with either *R. norvegicus* or *R. argentiventer.*

Although diverse in morphology, all the five species here compared with *R. hoffmanni* share several ecological and biogeographical features that set them apart from the murids endemic to Sulawesi. Not one of the five lives in undisturbed primary forest formations; all are restricted to habitats associated with human activity: cities, harbors, villages, agricultural fields, scrub, tropical gardens, and second-growth forest near villages and towns. In contrast to the indigenous murids occurring only on Sulawesi, that island is just a small part of the geographic range of each of the other five species and their presence on it suggests inadvertent transport there through human agency (Musser, 1977; Musser and Newcomb, 1983).

Rattus rattus: Nine scientific names have been applied to samples of house rats from Sulawesi and offshore islands: *dammermani* (Thomas, 1921), *palelae* (Miller and Hollister, 1921a), *lalolis* (Tate and Archbold, 1935), *toxi* (Sody, 1941), *makassarius* (Sody, 1941), *argyraceus* (Sody, 1941), *barussanoides* (Sody, 1941), *sapoensis* (Sody, 1941), and *pelengensis* (Sody, 1941). Available samples can be separated into three morphological groups. *Rattus rattus palelae* (includes *argyraceus* and *sapoensis*) occurs in northern and central Sulawesi and on the Togian islands. *Rattus rattus dammermani* (includes *lalolis, makassarius, toxi,* and *barussanoides*) is found on the southeastern and southwestern arms. *Rattus rattus pelengensis* is the house rat of Pulau Peleng. Furthermore, samples of the Sunda Shelf house rat, *R. r. diardii* (see Musser and Newcomb, 1983), have been obtained

←

row, an adult (AMNH 223720) from Gunung Kanino, 1500 m, in central Sulawesi is contrasted with the holotype, an adult, of *R. mollicomulus* (AMNH 101134) from 1500 m on Gunung Lompobatang in the southwestern peninsula to show the smaller size of the latter. Note also that the holotype is much smaller than the adult *R. hoffmanni* from Bantimurung; the specimen from Gunung Kanino, however, is about the same size as the adult from Kuala Navusu, reflecting the slight but nonsignificant differences in skull length between samples of *R. hoffmanni* from mountains and lowlands in central (see table 7) and northern (see discussion of *mollicomus* versus *hoffmanni* in text) Sulawesi.

TABLE 11

Contrasts between Adult *Rattus hoffmanni* and Sulawesian Samples of *Rattus rattus* and *Rattus nitidus* in External and Chromatic Traits

Trait	*R. hoffmanni*	*R. rattus*	*R. nitidus*
Head and body	Averages shorter than either *R. rattus* or *R. nitidus* (table 12)	Averages longer than *R. hoffmanni* (table 12)	Significantly longer than most samples of *R. hoffmanni* (table 12)
Upperparts	Pale to dark brown mixed with buff; fur soft, thick, and short; guard hairs inconspicuous, barely extending beyond overhairs	Dark brown; fur coarse and not as thick, with many stiff, spinelike hairs; guard hairs conspicuous and about three times length of overhairs	Grayish brown to dark brown, darker along back and grayer along sides; fur short, dense, and soft; guard hairs as in *R. hoffmanni*
Underparts	Gray to buffy gray; fur soft, dense, and short	Pale grayish buff to dark brownish buff; fur coarser and thinner	Gray (alters to pale yellow in some study skins); fur short, thick, and woolly
Feet	Brown or grayish brown with dark brown streak over metatarsal region	Length similar, but shorter relative to head and body (fig. 31); front and hind feet brown	Significantly longer than in any sample of *R. hoffmanni*; front and hind feet pure white
Tail	Dark brown everywhere; length about same as head and body (table 12)	Brown all over but paler; significantly longer than head and body (table 12) and much longer relative to head and body length (fig. 31)	Brown above, paler underneath; length equals or is shorter than length of head and body (table 12)
Mammae	8 (1 postaxillary pair, 1 abdominal pair, and 2 inguinal pairs)	10 (1 pectoral pair, 1 postaxillary pair, 1 abdominal pair, and 2 inguinal pairs)	12 (1 pectoral pair; 2 postaxillary pairs, 1 abdominal pair, and 2 inguinal pairs)

from Pulau Salayar (fig. 4) and some melanistic, long-tailed rats collected from harbors or docked ships have been identified as *R. r. rattus,* the European house rat (Sody, 1941: 267). Descriptions of these groups, records of their occurrence, and reasons for allocating the scientific names to *R. rattus* will be published later (Musser, in prep.).

Rattus hoffmanni and *R. rattus* are easily distinguished from each other by a combination of external features (table 11). Conspicuous cranial and dental contrasts also exist. Viewed in dorsal aspect, the most striking difference between them is in the interorbital and postorbital regions (fig. 26). In *R. hoffmanni,* margins of the interorbit are smooth and beveled, and the postorbit is bounded by low ridges. Comparable ridges outlining the interorbit and postorbit of *R. rattus* are higher and form angular shelves where the ridging passes from frontal to parietal bones. Furthermore, the interorbit is wider in *R. rattus,* both absolutely and relative to zygomatic breadth (fig. 31).

Seen in ventral view (fig. 27), the northern Sulawesian *R. rattus* has, on average, a longer bony palate and bulla relative to greatest length of skull, and an absolutely and relatively longer diastema than *R. hoffmanni* (table 12; fig. 31). The bony palate of *R. rattus,* measured between the first molars, is wider, both actually and relative to zygomatic breadth; the incisive foramina are narrower relative to their length; the mesopterygoid fossa is significantly narrower, especially in relation to zygomatic breadth (fig. 31); and the braincase is narrower. Most samples of *R. rattus* have gracile and smaller teeth than do samples of *R. hoffmanni*: toothrows are shorter (in actual value and also relative to length of skull) and molars narrower (as reflected by width of the first upper molar) (table 12; fig. 31). Finally, the anterior cingular margin of the first upper molar in *R. rattus* is smooth and unridged; either a prominent ridge or shelf outlines the cingular face of the molar in *R. hoffmanni* (fig. 28). These are the significant differences in craniodental dimen-

TABLE 12

Comparisons of Measurements (in millimeters) among Samples of Adult *Rattus hoffmanni*, *Rattus nitidus*, and *Rattus rattus* from Sulawesi

(Mean ± SD, range [in parentheses], and number of specimens are listed for each measurement)

		Northern Sulawesi		Pulau Malenge	
	R. nitidus[a]	*R. hoffmanni*[b]	*R. rattus*[c]	*R. hoffmanni*[d]	*R. rattus*
LHB	184.4 ± 8.9 (172–195) 5	170.1 ± 12.08 (144–200) 43	181.5 ± 3.00 (136–221) 43	190.3 ± 12.10 (175–208) 12	191.4 ± 13.20 (162–215) 23
LT	179.4 ± 9.04 (165–190) 5	169.5 ± 12.91 (150–192) 42	200.7 ± 15.30 (170–240) 41	164.2 ± 10.56 (147–183) 12	193.3 ± 11.30 (171–213) 23
LHF	39.8 ± 0.83 (39–41) 5	38.2 ± 1.44 (35–41) 59	37.5 ± 1.70 (35–42) 43	38.3 ± 1.49 (36–41) 12	37.9 ± 2.30 (36–40) 23
LE	18.5 ± 1.29 (17–20) 4	22.2 ± 2.31 (20–25) 20	21.9 ± 1.20 (20–24) 27	22.2 ± 0.7 (21–24) 12	21.7 ± 1.50 (19–26) 23
GLS	45.7 ± 1.49 (44.0–47.6) 4	42.5 ± 1.82 (37.7–46.1) 45	42.0 ± 2.17 (37.2–46.4) 41	42.7 ± 2.25 (39.6–47.6) 12	42.4 ± 1.88 (39.4–45.6) 23
ZB	20.4 ± 0.55 (19.6–21.0) 5	20.3 ± 0.87 (18.9–22.4) 47	19.6 ± 1.33 (16.6–23.0) 39	20.3 ± 1.22 (18.9–22.5) 12	19.3 ± 1.00 (17.8–21.2) 22
IB	6.7 ± 0.38 (6.4–7.3) 5	5.9 ± 0.28 (5.3–6.9) 60	6.2 ± 0.35 (5.6–7.0) 42	6.3 ± 0.31 (5.3–6.7) 12	6.0 ± 0.35 (5.3–6.7) 23
LR	14.6 ± 0.82 (13.5–15.5) 5	13.5 ± 0.77 (11.6–15.3) 60	13.1 ± 0.94 (11.2–15.2) 41	14.0 ± 1.10 (12.8–16.8) 12	13.1 ± 0.87 (11.3–14.8) 23
BR	8.2 ± 0.23 (8.0–8.6) 5	7.6 ± 0.40 (6.7–8.4) 56	7.3 ± 0.57 (6.2–9.0) 42	8.2 ± 0.43 (7.6–9.0) 12	7.6 ± 0.44 (6.7–8.5) 22
BBC	16.8 ± 0.21 (16.5–17.0) 5	16.5 ± 0.41 (15.5–17.5) 56	15.9 ± 0.67 (14.5–17.9) 41	16.5 ± 0.56 (15.5–17.2) 12	15.9 ± 0.47 (14.9–16.7) 23
HBC	11.7 ± 0.51 (11.1–12.4) 5	11.7 ± 0.49 (10.8–13.2) 46	11.6 ± 0.56 (10.4–12.9) 41	11.4 ± 0.43 (10.7–12.0) 12	11.0 ± 0.53 (10.0–12.0) 23
BZP	4.6 ± 0.30 (4.3–5.0) 5	4.8 ± 0.40 (4.0–5.8) 58	4.6 ± 0.48 (3.6–5.6) 43	5.2 ± 0.38 (4.5–5.7) 12	4.8 ± 0.09 (4.2–5.7) 23
LD	12.2 ± 0.86 (11.1–13.4) 5	11.1 ± 0.77 (9.3–12.4) 60	11.4 ± 0.88 (9.3–13.8) 43	11.2 ± 0.80 (10.0–12.8) 12	11.4 ± 0.55 (10.8–12.4) 22
LBP	8.8 ± 0.43 (8.1–9.2) 5	8.4 ± 0.44 (7.0–9.4) 59	8.4 ± 0.58 (7.1–9.6) 43	8.6 ± 0.37 (7.9–9.1) 12	8.5 ± 0.43 (7.8–9.4) 23
BBPM1	4.4 ± 0.28 (4.1–4.8) 5	3.8 ± 0.40 (3.1–4.5) 44	3.9 ± 0.40 (3.2–5.5) 43	3.9 ± 0.46 (3.2–5.8) 12	4.1 ± 0.39 (3.5–5.1) 23
LIF	8.6 ± 0.37 (8.0–9.0) 5	8.0 ± 0.52 (6.9–9.3) 60	8.1 ± 0.55 (6.9–9.0) 43	7.6 ± 0.66 (6.8–9.2) 12	8.1 ± 0.50 (7.4–8.8) 22
BIF	3.1 ± 0.20 (2.9–3.3) 5	2.8 ± 0.27 (2.0–3.6) 60	2.7 ± 0.30 (2.2–3.5) 43	3.0 ± 0.34 (2.7–3.7) 12	2.8 ± 0.27 (2.3–3.2) 22
LB	6.9 ± 0.11 (6.7–7.0) 5	6.9 ± 0.40 (6.0–7.7) 54	6.7 ± 0.65 (6.1–8.1) 42	6.9 ± 0.20 (6.6–7.3) 12	7.1 ± 0.28 (6.7–7.7) 22
CLM1–3	6.8 ± 0.20 (6.4–7.1) 5	7.3 ± 0.34 (6.4–7.7) 24	6.5 ± 0.30 (6.1–7.0) 44	7.0 ± 0.12 (6.8–7.1) 14	6.6 ± 0.21 (6.2–6.9) 23
BM1	2.1 ± 0.10 (2.0–2.2) 5	2.3 ± 0.12 (2.1–2.6) 60	1.9 ± 0.09 (1.8–2.1) 40	2.2 ± 0.05 (2.1–2.3) 12	1.9 ± 0.09 (1.8–2.1) 22

[a] USNM 219687–219691, the type series of *R. hoffmanni subditivus*.

[b] Localities 1, 9, and 14 (see fig. 6 and gazetteer).

[c] Bumbulan, Molinggapoto, Pulau Paleleh, and Tolitoli.

[d] Locality 99 (see fig. 6 and gazetteer).

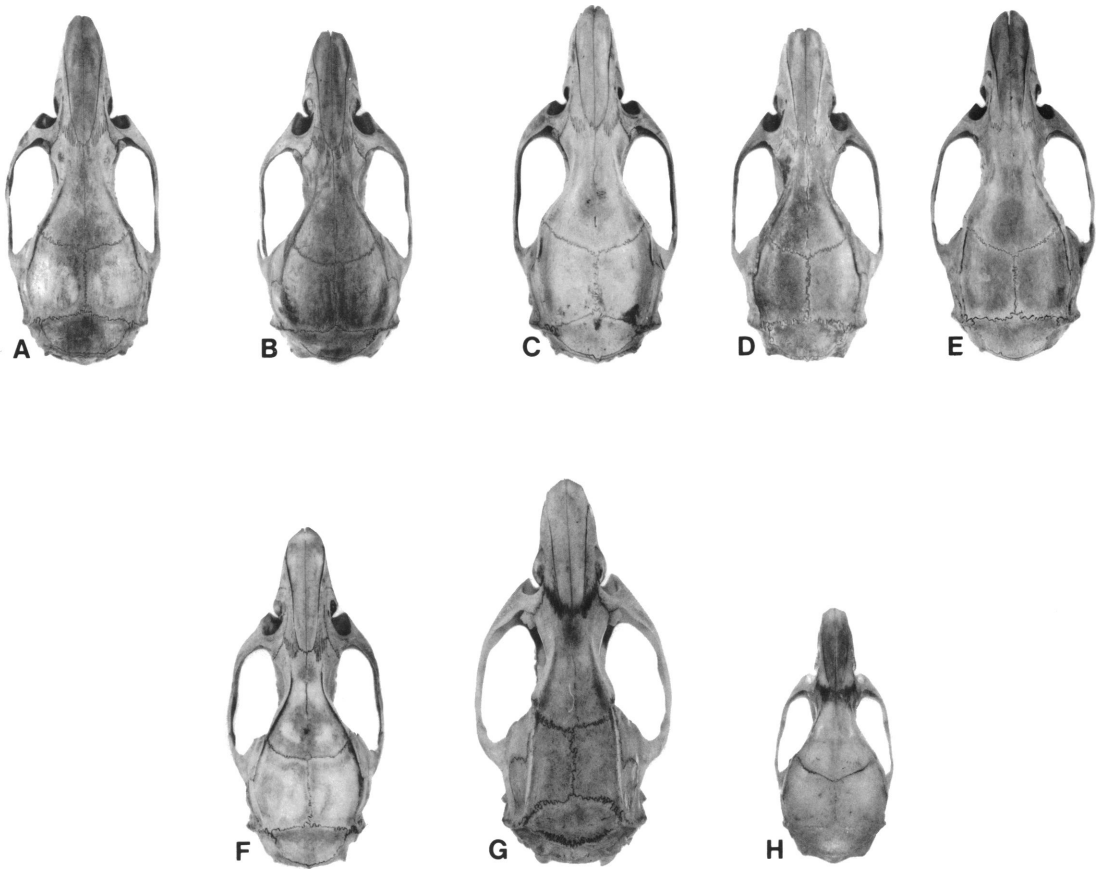


Fig. 26. Dorsal views (×1) of adult crania comparing *Rattus hoffmanni* from northern Sulawesi (**B,** USNM 219583) with samples of nonendemic species of *Rattus* occurring on Sulawesi. **A.** *R. nitidus,* central Sulawesi (USNM 219688). **C.** *R. rattus palelae,* Bumbulan, northern Sulawesi (AMNH 153004). **D.** *R. r. palelae,* Pulau Malenge, Togian Islands (AMNH 153331). **E.** *R. r. dammermani,* southwestern Sulawesi (MZB 4256). **F.** *R. argentiventer,* Bali (AMNH 107543). **G.** *R. norvegicus,* Taiwan (AMNH 185196). **H.** *R. exulans,* central Sulawesi (AMNH 215290).

sions, proportions, and qualitative features that we found between samples of the two species from most regions of Sulawesi; Pulau Malenge is an exception.

The differences between *R. hoffmanni* and *R. rattus* on Pulau Malenge are of the same kind and degree as occur between the species over most of the mainland (figs. 26, 27). The only exception is that *R. hoffmanni* from Malenge has a significantly longer rostrum and a wider braincase than *R. rattus* from that island. The molar rows of *R. hoffmanni* are usually longer than those of *R. rattus,* but the Malenge *R. hoffmanni* have shorter rows than do most samples of *R. hoffmanni* from the mainland, which results in there being no significant differences in length of toothrow between the two species on the island. *Rattus hoffmanni* still has wider teeth, however, and each upper molar is significantly wider than that in *R. rattus* (table 12).

Rattus nitidus: Five specimens representing this species were collected in central Sulawesi by H. C. Raven in 1917: one from Tuare (USNM 219691), one from Watutau in Napu Valley (USNM 219687), and three from Gimpu (USNM 219688–219690). These rats, along with another one from Watutau (USNM 219615), were identified by Miller and Hollister (1921a: 70) as *R. hoffmanni.*

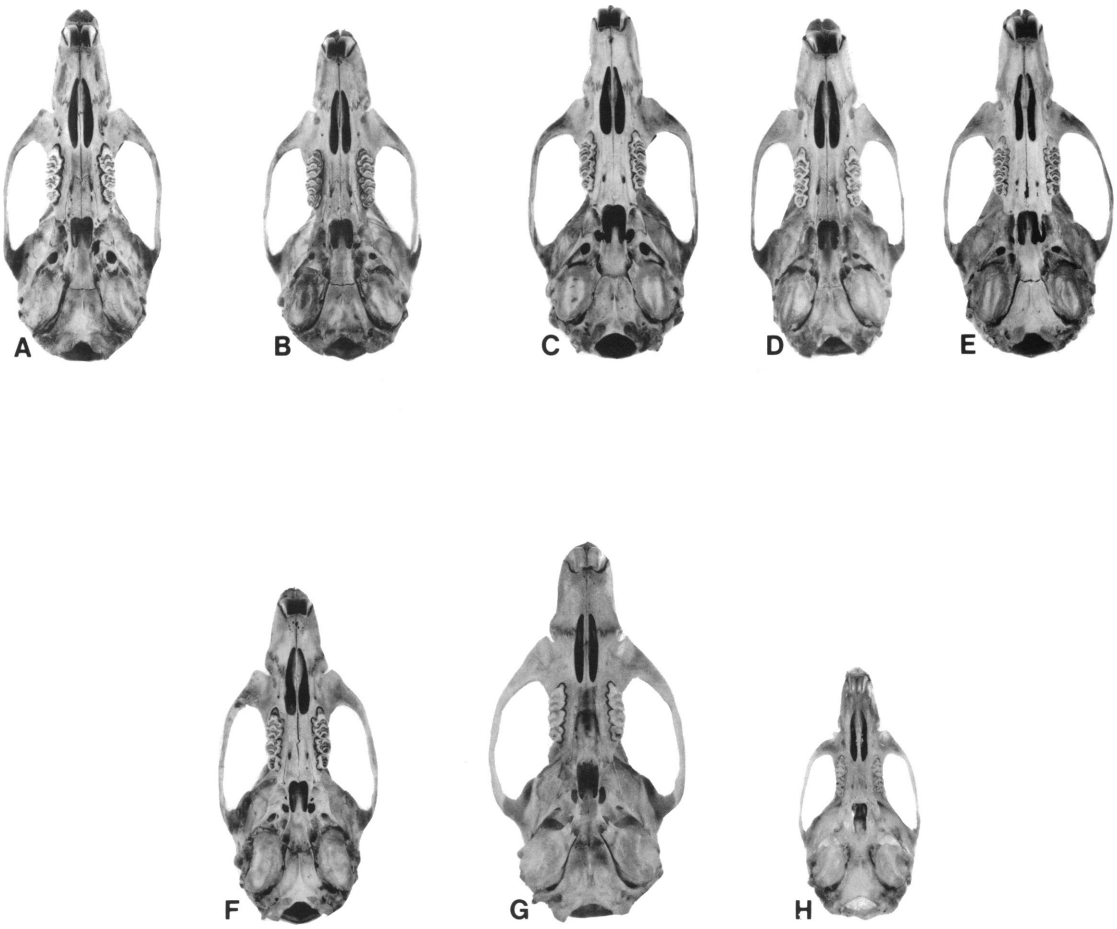


Fig. 27. Ventral views (×1) of crania from same specimens illustrated in figure 26. *Rattus hoffmanni* (**B**) is compared with *R. nitidus* (**A**), *R. rattus* (**C-E**), *R. argentiventer* (**F**), *R. norvegicus* (**G**), and *R. exulans* (**H**).

They thought the small sample to be so distinct from specimens of what they considered to be typical *R. hoffmanni* from northern Celebes, and from their material of *R. hoffmanni* from the central part of the island, that they proposed the name *R. h. subditivus* for them. Actually, USNM 219615, from Watutau, is the only one of the six specimens that is an example of *R. hoffmanni*. It is a very young adult and is indistinguishable from other *R. hoffmanni* of comparable age that Raven collected in central Sulawesi, and that Miller and Hollister (1921a: 70) later named and described as *R. h. linduensis*. Since Raven's survey in 1917, additional specimens of *R. nitidus* have been collected from Napu Valley at Tamadue, 1067 m (AMNH 229611, 229612). The species has also been discovered in mountain valleys in the southern part of central Sulawesi, where samples come from Kantewu, 1000 m (AMNH 229622–229637); Kalamanta, 1100 m (AMNH 229619–229621); Bangko, 1400 m (AMNH 229613–229618); Tedeboe, 1280 m (AMNH 229642–229648); Parahaleang, 1195 m (AMNH 229638, 229639); and Singkalong, 1210 m (AMNH 229640, 229641). *Rattus nitidus* is known to occur only in high valleys in central Sulawesi, where it lives around village houses and nearby scrub and gardens; the species has never been collected from undisturbed primary forest.

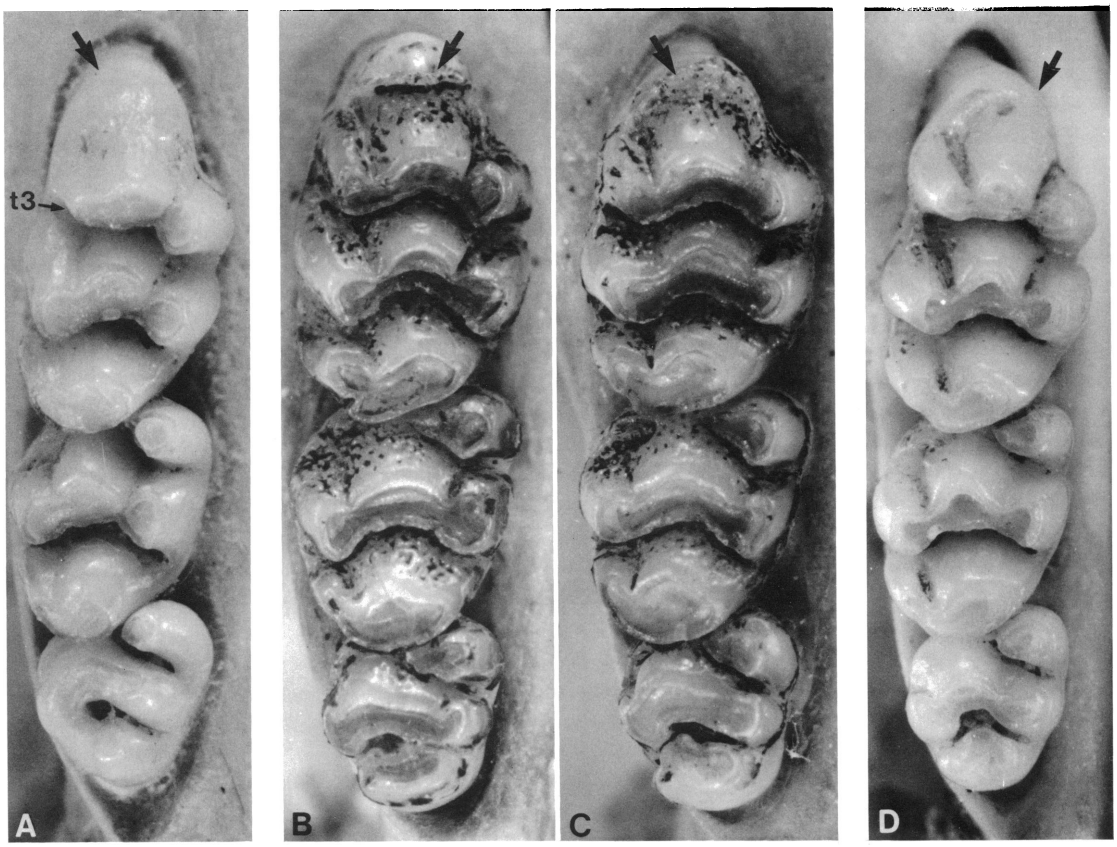


Fig. 28. Occlusal views of right upper molar rows from Sulawesian species of *Rattus* illustrating variation in form of anterior cingulum and cusp t3 of M1. **A.** *R. nitidus,* central Sulawesi (AMNH 229633; CLM1–3 = 7.2 mm); face of the anterior lamina (arrow) is smooth, cusp t3 either is indistinct or appears absent in some specimens. **B.** *R. hoffmanni*, central Sulawesi (AMNH 223393; CLM1–3 = 7.7 mm); front margin of tooth is thrown up into a transverse, cingular cusplike ridge (arrow), and cusp t3 is discrete and not broadly connected to cusp t2. **C.** *R. hoffmanni*, central Sulawesi (AMNH 223390; CLM1–3 = 7.5 mm); a shelflike ridge (arrow) outlines anterior margin of the tooth. **D.** *R. rattus,* northeastern Sulawesi (AMNH 101272; CLM1–3 = 6.6 mm); anterior cingulum is smooth (arrow) and without either a prominent ridge or a cusp, and cusp t3 is a large and prominent component in the first row of cusps. The form of the anterior cingulum and cusp t3 as shown in these examples of *R. nitidus* and *R. rattus* is characteristic of each of these species. All specimens of *R. hoffmanni* that we studied possess a cingular ridge or shelf, and these surfaces support either a large cusplet or several small cusplets in 12 percent of the samples.

Rattus nitidus is part of the rodent fauna of Southeast Asia. Its distributional range extends from the mountains of northeastern India through Burma, Thailand, southern China, and Laos to North and South Vietnam (fig. 29). It has also been recorded from northern Luzon in the Philippines (Musser, 1977), from the island of Seram in the Malukus, from the Vogelkop region of Irian Jaya (Taylor et al., 1982), and from the Palau Islands, east of the southern Philippines (fig. 30). The identification of *subditivus* as *R. nitidus* and documentation supporting the geographic distributions shown in figures 29 and 30 will be presented in a report being prepared (Musser, in prep.). *Rattus nitidus* is apparently one of several species to have dispersed from its indigenous range on mainland Asia to the Philippines, Sulawesi, and through the Indo-Australian region by human agency, proba-

bly by accident; it is certainly a foreign component of the Sulawesian rodent fauna.

About as large as house rats, *R. nitidus* has dark, brownish gray upperparts and gray underparts. The fur is short, thick, and soft. The tail is about the same length as the head and body, often shorter but rarely longer. Dorsal surfaces of the front and hind feet are white. Females have 12 mammae: one pectoral pair, two postaxillary pairs, one abdominal pair, and two inguinal pairs. The skull is large and angular. The combination of long nasals and rostrum, wide interorbital, wide boxlike braincase, and small bullae is distinctive. The anterolabial cusp of each first upper molar, so well developed and conspicuous in most species of *Rattus,* is either absent or represented only by a low bulge in *R. nitidus.*

External features of *R. hoffmanni* and *R. nitidus* are contrasted in tables 11 and 12. In fur color and texture, *R. nitidus* resembles *R. hoffmanni* more closely than do house rats. When Miller and Hollister (1921a: 71) described *R. h. subditivus,* they diagnosed the taxon as "Larger and lighter colored than *Rattus hoffmanni hoffmanni* or *R. h. linduensis*; grayer, less rufous or rich dark brown; underparts lighter, with strong suffusion of pale yellowish rather than grayish drab. Skull larger than in *linduensis,* as large as in typical *hoffmanni.*" The pelage contrasts constitute some of the external differences separating *R. hoffmanni* and *R. nitidus* (table 11). *Rattus nitidus* also has much smaller ears than *R. hoffmanni,* both in absolute value and relative to length of head and body (table 12; fig. 31).

Differences between the two species in configuration of the cranium are evident in figures 26 and 27. Skulls of *R. nitidus* are larger—as Miller and Hollister (1921a) noted—and appear more streamlined. The braincase is boxlike and the interparietal bone is longer and wider. The teeth are conspicuously smaller—not massive as they appear in *R. hoffmanni.* Cusp t3 on each first upper molar is well developed and conspicuous in *R. hoffmanni,* but so broadly coalesced with cusp t2 that it either appears absent or is indicated by only a swelling in *R. nitidus* (fig. 28). Either a ridge or shelf (which supports cusplets in some specimens) outlines the anterior cingular margin of the first molar in *R. hoffmanni*; the cingular margin is smooth in *R. nitidus* (fig. 28).

Rattus nitidus differs significantly from all samples of *R. hoffmanni* in several cranial and dental dimensions (table 12). The cranium of *R. nitidus* is, on average, longer; the interorbital region is wider; the rostrum, diastema, and bony palate are longer; the incisive foramina are longer and wider; the bony palate at the level of the first molars is wider; and each first upper molar is narrower. In addition, the toothrows of *R. nitidus* are shorter than those in all samples of *R. hoffmanni* but the ones from southwestern Sulawesi and Pulau Malenge. No significant differences were found between *R. nitidus* and samples of *R. hoffmanni* in means of any of the other cranial measurements. Proportional contrasts and similarities between the two species are illustrated in figure 31.

Rattus exulans: Four scientific names have been tied to samples of this species from Sulawesi: *aemuli* (Thomas, 1896), *raveni* (Miller and Hollister, 1921a), *eurous* (Miller and Hollister, 1921a), and *malengiensis* (Sody, 1941). *Rattus exulans* occurs throughout Sulawesi wherever primary forest has been altered or removed, and is one of the most abundant mammals in these disturbed habitats. We contrast *R. exulans* with *R. hoffmanni* because young adults and juveniles of the latter have been frequently misidentified as *R. exulans* in collections in museums. At least one taxon, *R. tatei,* has been described based on young adults of *R. hoffmanni* (Musser, 1971) and was thought to be related to *R. exulans* by its original describer (Ellerman, 1941) and other workers (Laurie and Hill, 1954).

Examples of the two species are easily distinguished by size, color, distribution of mammary glands, and dental measurements. Adults of *R. exulans* are about half the size of *R. hoffmanni* of comparable age (table 13; figs. 26, 27). Female *R. exulans* have four pairs of mammae (one pectoral, one postaxillary, and two inguinal) in contrast to the single postaxillary pair, one abdominal pair, and two inguinal pairs possessed by *R. hoffmanni.* Juveniles and very young adults of *R. hoffmanni* resemble adult examples of *R. exulans* in some external features, but the two species can be separated by color of under-

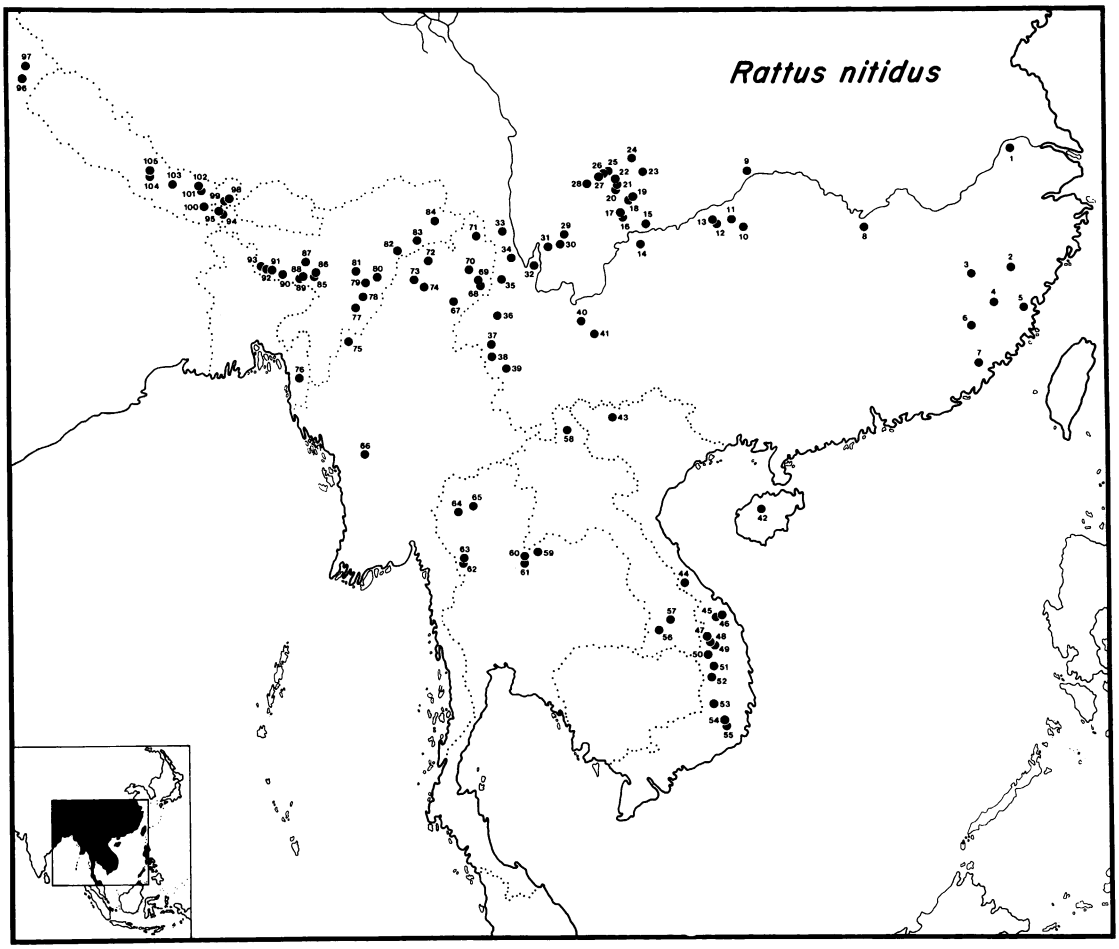


Fig. 29. The geographic distribution of *Rattus nitidus* in China (1–42), Vietnam (43–55), Laos (56–58), Thailand (59–65), Burma (66–75), Bangladesh (76), and India (77–105). Possibly this scatter estimates most or all of the indigenous range of the species.

parts of head and body, length of toothrows, and dimensions of individual teeth. For example, the underparts of young *R. hoffmanni* are dark gray, but adult *R. exulans* have white or grayish white venters. Crown length of the maxillary toothrow in *R. exulans* is short (table 13), and the breadth of each first upper molar rarely exceeds 1.6 mm—a conspicuous contrast to the long toothrows of *R. hoffmanni* and their wider first upper molars, teeth that exceed 2.0 mm in width.

Rattus norvegicus: In Sulawesi, the Norway rat is found in seaports and is not native to the island. We have no evidence that it and *R. hoffmanni* occur together in the same habitat, but specimens of each could be confused in museum collections. Examples of *R. norvegicus* have a much larger head and body than do specimens of *R. hoffmanni* of comparable age, the tail is always shorter than the length of head and body and is bicolored (brown above, gray below), feet are longer and dorsal surfaces are white, and females have 12 mammae (one pectoral pair, two postaxillary pairs, one abdominal pair, and two inguinal pairs). Crania of *R. norvegicus* are larger and more robust than those of *R. hoffmanni,* and the ridges bounding the dorsolateral margins of the braincase form a rectangle and are unlike the curved outline in *R. hoffmanni* (fig. 26). In each first upper molar of *R. norvegicus,* cusp t3 is either absent or

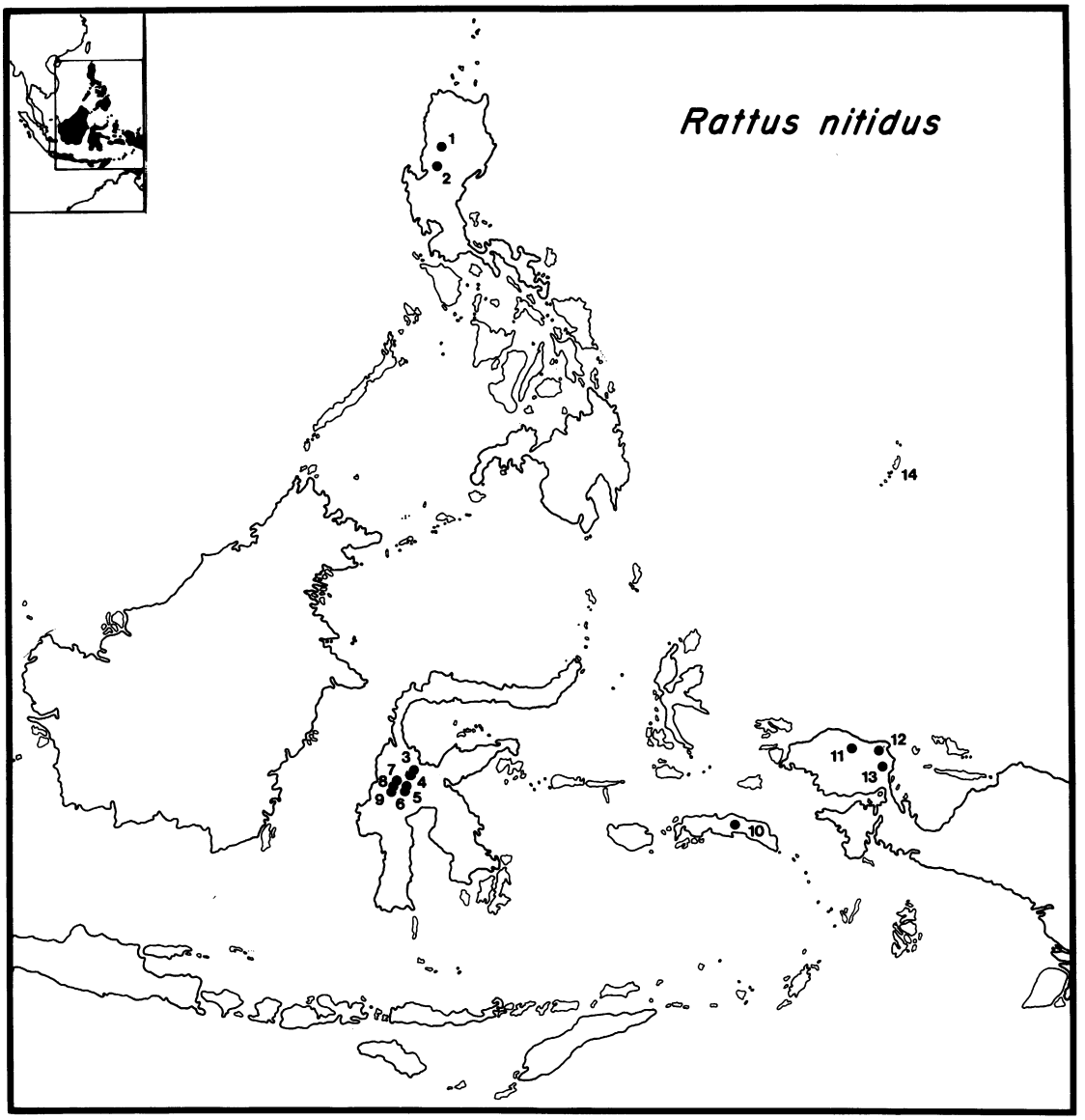


Fig. 30. The geographic distribution of *Rattus nitidus* east of the Sunda Shelf on Luzon in the Philippines (1, 2), Sulawesi (3–10), Seram (10), Irian Jaya (11–13), and the Palau Islands (14). This insular pattern likely reflects distributional processes mediated by human agency.

represented by a slight bump, a dental feature that separates every specimen of *R. norvegicus* we have examined from every example of *R. hoffmanni,* which has a large and conspicuous cusp t3.

Rattus argentiventer: The ricefield rat on Sulawesi was originally described as *Rattus pesticulus* (Thomas, 1921); its identification with *R. argentiventer* was documented by Musser (1973). Sulawesi is just one place within the broad geographic range of *R. argentiventer.* The species is part of the mainland Indochinese fauna, occurs on the Malay Peninsula and on the large islands and a few smaller ones on the Sunda Shelf, is scattered through Nusatenggara, has been recorded from Mindoro and Mindanao in the Philippines, and was carried all the way east to Irian

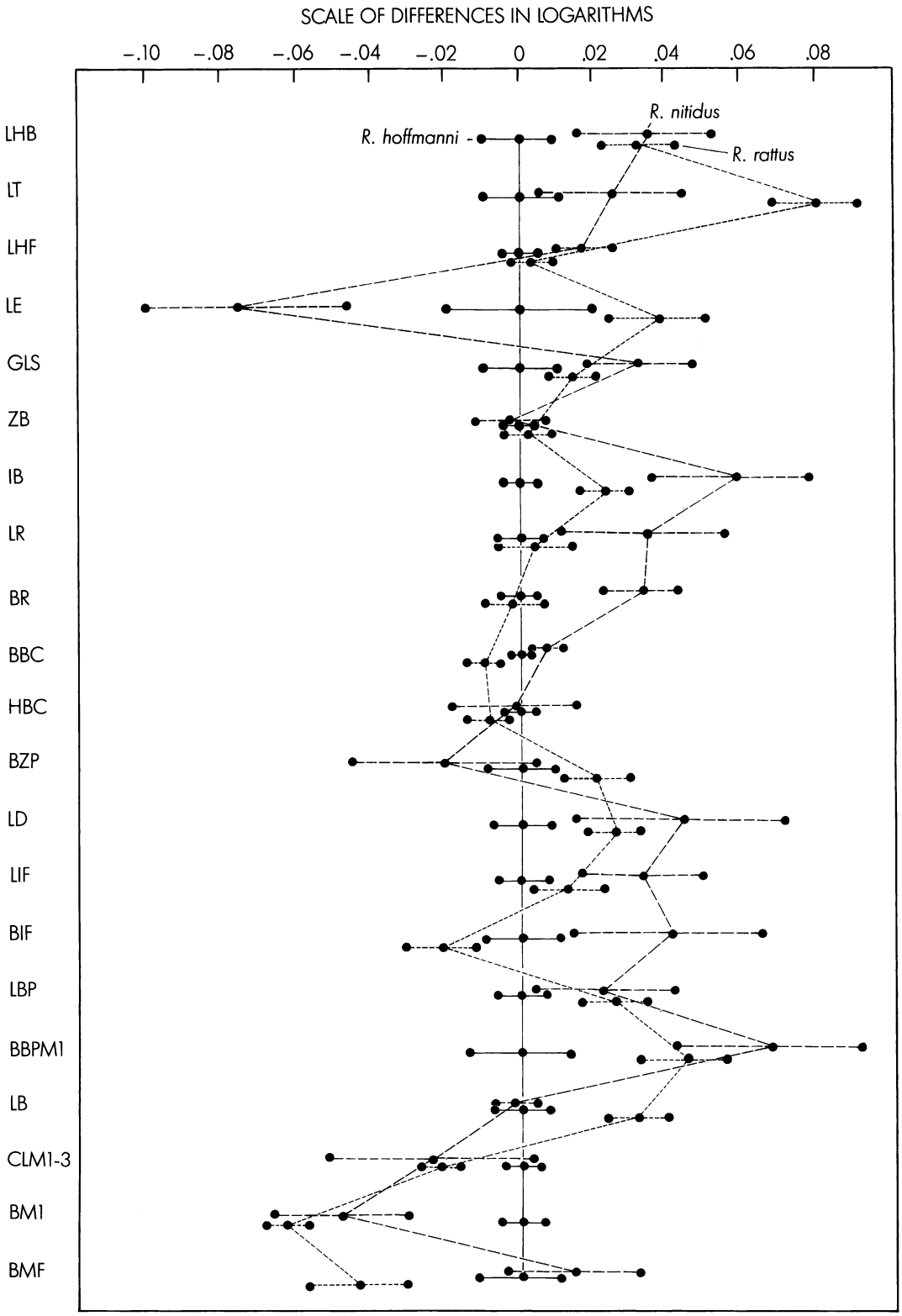

SCALE OF DIFFERENCES IN LOGARITHMS
−.10
−.08
−.06
−.04
−.02
0
.02
.04
.06
.08
R. nitidus
R. hoffmanni
R. rattus
LHB
LT
LHF
LE
GLS
ZB
IB
LR
BR
BBC
HBC
BZP
LD
LIF
BIF
LBP
BBPM1
LB
CLM1-3
BM1
BMF

TABLE 13

Comparison of Measurements (in millimeters) between Adult *Rattus hoffmanni* and the Nonendemic *Rattus exulans* and *Rattus argentiventer* of Sulawesi

(Mean ± SD, range [in parentheses], and sample size are given for each measurement)

	R. hoffmanni[a]	*R. exulans*[b]	*R. argnetiventer*[c]
LHB	170.1 ± 12.08 (144–200) 43	117.3 ± 7.08 (103–134) 47	174.0 ± 11.78 (157–193) 11
LT	169.5 ± 12.91 (150–192) 42	131.6 ± 7.46 (117–148) 41	162.8 ± 13.45 (141–186) 11
LHF	38.2 ± 1.44 (35–41) 59	22.3 ± 1.02 (25–30) 47	35.7 ± 2.53 (32–40) 11
LE	22.1 ± 2.31 (20–25) 20	18.0 ± 0.81 (17–20) 47	18.8 ± 1.60 (15–21) 11
GLS	42.5 ± 1.82 (37.7–46.1) 45	30.7 ± 0.76 (28.7–32.0) 45	–
CLM1–3	7.3 ± 0.34 (6.4–7.7) 24	5.0 ± 0.19 (4.5–5.4) 43	6.9 ± 0.99 (6.4–7.3) 15
BM1	2.3 ± 0.12 (2.1–2.6) 60	1.5 ± 0.08 (1.3–1.6) 43	2.2 ± 0.08 (2.0–2.3) 15

[a] Localities 1, 9, and 14 (see fig. 6 and gazetteer).
[b] Sample is from Tomado, 1000 m, central Sulawesi.
[c] Samples are from central and south-central Sulawesi.

Jaya (Musser, 1973). The ricefield rat is clearly not a native element of the endemic mammalian faunas found in most of these spots; possibly the species is indigenous to mainland Indochina and may have spread through the Indo-Malayan and Indo-Australian regions along with the geographic expansion of rice culture (Musser and Newcomb, 1983).

Excluded from primary tropical forest formations and restricted to lowlands (below 300 m) on Sulawesi, *R. argentiventer* is found in ricefields (where it sometimes becomes a major pest), fallow agricultural fields, and wasteland overgrown by grass and low shrubs (see Musser, 1973, for a fuller account of the kinds of habitats in which these animals live). On Sulawesi, the species is clearly not part of the endemic diversity of murid species and can exist only in places where the primeval forest cover has been removed and agricultural activity persists. Compared to *R. rattus* and *R. exulans,* which are common in disturbed areas, *R. argentiventer* is either uncommon or simply not caught as frequently; there are few specimens of the ricefield rat available for study, compared with the hundreds of individuals of the other two species. Examples of *R. argentiventer* have been taken in the northeastern arm (Menado, BMNH 21.2.9.11, 21.2.9.22), in central Sulawesi (Leda, AMNH 229526, 229527; Omu, AMNH 229529; Pakuli, AMNH 229530, 229531; Pulu, AMNH 229532; and Sibalaya, AMNH 229533, 229537), and in the south (Muktisari, AMNH 229539; Tawibaru, AMNH 229540–229542; Teromui, AMNH 229543, 229544; Wasuponda, AMNH 229545; Luwu, MZB 6412–6414; Ujung Pandang, MZB 4227; and Bulukumba, MZB 9005–9907).

Rattus hoffmanni and *R. argentiventer* resemble one another in body size (table 13), but are otherwise very different. Compared with samples of *R. hoffmanni,* specimens of *R. argentiventer* have coarser pelage, upper-

←

Fig. 31. Ratio diagram. Dimensions are compared among samples of *Rattus hoffmanni* (the standard), *R. rattus,* and *R. nitidus* from Sulawesi.

parts that are much paler (buffy or yellowish brown speckled with black), silvery gray underparts, dorsal surfaces of hind feet that are whitish gray with a pale medial brown strip, pale brown (tan) ears, an orange tuft of hairs in front of each ear, pale brown tail that is usually much shorter than head and body, and six pairs of mammae (one pectoral, two postaxillary, one abdominal, and two inguinal). External features of *R. argentiventer* are very distinctive, and the combination of speckled yellowish brown upperparts, ochraceous ear tufts, silvery gray underparts, short tail relative to length of head and body, pale ears and tail, and six pairs of mammae easily distinguish the species not only from *R. hoffmanni* but from any other *Rattus* known to occur on Sulawesi.

Crania and molars of *R. argentiventer* and *R. hoffmanni* resemble one another in shape and proportions (figs. 26, 27). The ricefield rat has, on average, a wider rostrum and deeper zygomatic notches, more spacious incisive foramina, more inflated bullae relative to cranial size, and shorter toothrows, but molars that average as wide as those in *R. hoffmanni,* making them much wider relative to toothrow length. In addition, about one-fourth of the specimens in any sample of *R. argentiventer* have an anterocentral cusp at the front of each first lower molar; a comparable structure is not present on the teeth in *R. hoffmanni.*

Comparisons with Endemic *Rattus*

Here we contrast our samples of *R. hoffmanni* with those drawn from two other populations of the genus, *R. tawitawiensis* and *R. elaphinus.*

Rattus tawitawiensis: This endemic of Tawitawi Island is represented by three specimens that were described by Musser and Heaney (1985). Because they saw certain morphological similarities between the Tawitawi rat and *R. hoffmanni,* Musser and Heaney compared the two species and concluded (p. 17) that in "pelage features, number of mammae, many aspects of cranial conformation, and dental characteristics, specimens of *R. tawitawiensis* and *R. hoffmanni* are similar. There are differences, however, and these are of the same magnitude that we have found to distinguish other species of *Rattus* from one another. There is no evidence from our samples that the series from Tawitawi Island represents an insular subspecies of *R. hoffmanni,* even though the two species share many morphological features, including four pairs of mammae and relatively large molars."

The two species do resemble each other in fur coloration and number of mammae, but *R. tawitawiensis* is a much larger animal than *R. hoffmanni.* In addition, the Tawitawi rat has a wider and shorter rostrum (relative to cranial size), heavier ridging bounding the postorbital and temporal margins, much deeper cranium, a more expansive interparietal, conspicuously wider incisive foramina, smaller bullae relative to cranial size, and enamel ridges along posterior margins of labial cusps on the first and second upper molars (see figs. 10 and 11 in Musser and Heaney, 1985). These distinctions separate the three specimens of *R. tawitawiensis* from specimens in every sample of *R. hoffmanni* that we examined. Our new comparisons only reinforce the view expressed by Musser and Heaney: no evidence exists from which to infer that *R. hoffmanni* and *R. tawitawiensis* are insular morphological equivalents of each other or even that they are very closely related.

Rattus elaphinus: Named and described by Sody in 1941 (p. 307), *R. elaphinus* was based on specimens obtained in September and October 1938 by J. J. Menden from the "plains" of Pulau Taliabu, the largest of the Sula Islands, the archipelago east of Pulau Peleng (fig. 4). Sody examined 12 specimens (MZB 4076–4087) that were housed in the Museum Zoologicum Bogoriense in Bogor. Menden had actually collected at least 33 specimens: 12 were deposited in the museum at Bogor, 18 (AMNH 109318–109335) were sent to the American Museum of Natural History, and 3 (SMT 11343–11345) were given to the Staatliches Museum für Tierkunde at Dresden. We have studied the 33, including the holotype (MZB 4087); all represent the same species.

To Sody, *R. elaphinus* was characterized (p. 307)

> by the handsome, smooth rufous buff colour of the back, a very fine mixture of this colour with black.

The dorsal fur is rather dense and moderately long, consisting of woolly hairs (grey with ochraceous buff tips, which make perfectly invisible the grey), between which, on whole back and sides, an abundance of longer piles, black, on the sides with light tips. No spines. Ventral side ochraceous gray, rather dark, sometimes flecked with castaneous, especially on chin and chest. Sometimes the ventral colour rather strongly reminds *R. whiteheadi.* Tail black, rings 10–11 per cm. Mammae: pectoral 2 pairs (but anterior extremely difficult to discover), inguinal ones 2 pairs.

Sody listed some external and cranial measurements for the holotype, and provided ranges for lengths of toothrows and percentages of tail length relative to length of head and body.

Sody did not compare his sample of *elaphinus* with any other kind of *Rattus,* and the nature of the species has been obscure since it was first described. Laurie and Hill (1954), for example, in their list of mammals of New Guinea, Celebes, and adjacent areas, treated *R. elaphinus* as incertae sedis.

Judged by morphology of skin and skull, *R. elaphinus* is distinctive. Specimens of it average longer than examples of *R. hoffmanni* (table 14), but like *R. hoffmanni,* the tail of *R. elaphinus* is usually shorter than the length of head and body (sometimes about the same length) and is similar to *R. hoffmanni* in color and scalation. *Rattus elaphinus* has shorter hind feet than most specimens of *R. hoffmanni* (table 14).

In texture and color of pelage, *R. elaphinus* and *R. hoffmanni* are unlike one another. The Taliabu rat has very short, dense, and soft fur over the upperparts, a coat that is velvety to the touch. Along the back and rump, the overhairs range from 10 to 15 mm long and guard hairs project beyond the overfur by only 5–10 mm; their short lengths combined with the buffy tip on many of them render the guard hairs nearly indistinguishable from the layer of overhairs. *Rattus hoffmanni* does not have velvety fur, and although the guard hairs are short, most are all black (few are tipped with buff) and they are far more conspicuous.

Sody accurately described the color of the dorsal coat in *R. elaphinus.* The variation ranges from an even, brownish orange to a brownish orange lightly suffused with short black streaks, a pattern that begins to approach but is far from the agouti effect seen in *R. hoffmanni.* Hairs along the dorsal part of the head and body have gray bases and brownish orange tips. The gray bases do not show through in many specimens: thus is produced the even brownish orange of the upperparts. This warm, rich hue becomes paler along the sides of the head and body; here the hairs are gray with pale buffy tips. The grayish buff of the sides merges imperceptibly with the grayish buff of the underparts.

The ventral fur of adult *R. elaphinus* is also short, dense, and soft. The color is gray washed with buffy to ochraceous hues. At one extreme in the sample are five specimens with gray underparts lightly tinged with pale buff; the tone is brighter in axillary and inguinal regions. At the other extreme are three specimens that have gray underparts washed with orange-red on the chin, throat, chest, and inguinal regions. The other specimens in the series before us are intermediate between these two extremes and connect, in a continuous fashion, those with primarily gray underparts tinged with buff to those that are gray and washed with reddish orange.

Upper surfaces of the front and hind feet are brown, the claws are cream, and the long hairs at the base of each claw are silvery white. The ears are pigmented and haired like *R. hoffmanni,* and the eyelids are black.

Sody's count of the mammary glands was correct; on every female we examined there are eight mammae: one pectoral pair, one postaxillary pair, and two inguinal pairs (no abdominal pair). *Rattus hoffmanni* also has eight mammae, but lacks a pectoral pair and has an abdominal pair.

Of the 33 specimens, 30 are in adult pelage and only 3 (MZB 4076, 4079, 4080) have some juvenile fur. In those individuals, the juvenile coat was being replaced by adult pelage when the rats were trapped. Juvenile pelage is soft and thick. Upperparts are grayish brown suffused with chestnut. The underparts range from ochraceous gray to buffy gray.

The shape of the skull in *R. elaphinus* resembles that of *R. hoffmanni,* but the two species differ in dimensions and proportions. Skulls of each are contrasted in figure 33, absolute differences and similarities between mean values of measurements are listed in

table 14, and proportional differences and similarities between dimensions in the two species are illustrated in figure 34. The most conspicuous cranial differences between the two are in dimensions of the interorbital area and lengths of rostrum, palate, and bulla. In *R. elaphinus,* the skull, rostrum, and diastema average significantly longer than in most samples of *R. hoffmanni. Rattus elaphinus* also has a wider interorbital area and rostrum, and wider incisive foramina than most other samples of *R. hoffmanni.* The difference in breadth of the interorbital region is especially conspicuous; not only is it actually significantly wider ($P < 0.01$) than in any sample of *R. hoffmanni,* but it is also wider relative to breadths of zygoma, rostrum, incisive foramina, and braincase (fig. 34).

The palatal region is distinctive in *R. elaphinus.* The bony palate is significantly longer and wider than in samples of *R. hoffmanni*; it is not only actually longer, but longer relative to greatest length of skull. The toothrows in *R. elaphinus* are about the same length as those in most samples of *R. hoffmanni,* and the difference in length of the bony palate between the two species is due to the shelflike extension of the palatal bridge beyond back surfaces of the third molars. For example, the mean of this projection (from molar backs to posterior edge of palate) in the sample of *R. elaphinus* is 2.3 mm, which is significantly ($P < 0.01$) longer than in a sample of *R. hoffmanni* represented by a series of Teteamoet, in which the mean is 1.2 mm (table 14); the distance from the back of the third molar to the posterior margin of the bony palate rarely exceeds 2.0 mm in any specimen of *R. hoffmanni.* Finally, the mesopterygoid fossa averages wider in *R. elaphinus* than in any sample of *R. hoffmanni.*

The bullae of *R. elaphinus* differ conspicuously in size and proportions from those of *R. hoffmanni.* They are absolutely shorter than in most samples of *R. hoffmanni* and shorter relative to greatest length of skull.

The toothrows of *R. elaphinus* are, on average, about the same length as the average values in about half the samples of *R. hoffmanni*; they are, however, significantly shorter than the mean for samples from Gunung Klabat and southeastern Sulawesi and, as in most samples of *R. hoffmanni,* are significantly longer than the average for samples from southwestern Sulawesi and Pulau Malenge (compare table 14 with tables 5, 6, and 9). Although the two species are similar in actual length of toothrows, they are proportionately dissimilar. For example, relative to greatest length of skull, and especially to length of bony palate, the molar rows in *R. elaphinus* are significantly shorter than in *R. hoffmanni* (fig. 34). Dimensions of the first upper molars are also different; in series of *R. elaphinus,* they average narrower than in some samples of *R. hoffmanni.* The only important differences between the two species reflected in cusp patterns are the lack of both a posterior cingulum on each first upper molar and cusp t3 on each third upper molar in *R. elaphinus*; some expression of a posterior cingulum is found in about half of every sample of *R. hoffmanni* and a cusp t3 occurs on third molars at a low frequency.

THE SPECIES FROM PULAU PELENG

Rattus hoffmanni occurs throughout mainland Sulawesi and has been recorded from Pulau Lembeh, off the tip of the northeastern peninsula, and Pulau Malenge, part of the Togian islands in Teluk Tomini, but is not known from Pulau Peleng in the Banggai Islands. On Pulau Peleng, a large island off the east coast of central Sulawesi, resides a species that is represented by only one specimen collected in 1938 by J. J. Menden. The individual is not a member of either *R. rattus pelengensis* or *R. foramineus pelurus* (= *R. pelurus*), forms that were named and described by Sody in 1941 on the basis of material collected by J. J. Menden from Pulau Peleng; nor is it related to *R. exulans,* the third and last of the species of *Rattus* recorded from the island. Instead, the specimen is a sample of an island population that in some characters resembles *R. hoffmanni* more closely than it does any other described *Rattus.* But, it is not a morphological and insular counterpart of *R. hoffmanni.* From what we can observe from study of skin, skull, and dentition, the specimen is unlike those in samples of *R. hoffmanni* in many aspects of its morphology, so distinctive in fact that we

hypothesize it represents a species until now without a name, known only from and probably endemic to Pulau Peleng.

Describing the morphology of the new species forms one aspect of its definition; contrasting that morphology with characteristics of other species of *Rattus* whose identities have been recorded in the systematic literature completes the morphological identity and documentation of the distinctions that set the Peleng rat apart from all other known species of the genus. Early in our study, we compared the holotype with samples of all the species now placed in *Rattus* (see the list in table 57 in Musser and Newcomb, 1983: 572) that are native to India, Asia, and the Indo-Malayan and Indo-Australian regions, and concluded very quickly that to define the new form would require comparisons with four groups of *Rattus*. The first comparisons are with *R. hoffmanni,* because that species is morphologically similar to the Peleng animal and is the best representative of the genus *Rattus* on Sulawesi, the nearest landmass to the west of Pulau Peleng; we incorporate these comparisons in the description of the new species.

We then contrast the holotype from Peleng with the species of *Rattus* already recorded from the island—*R. exulans, R. rattus,* and *R. pelurus*—so that any future surveyors of mammals on Pulau Peleng will be able to identify the new rat.

The third set of contrasts is between the Peleng rat and *R. elaphinus* from Pulau Taliabu, the largest island in the archipelago just east of Pulau Peleng. Taliabu is the first known place to the east of Peleng from which a native species of *Rattus* has been described; furthermore, that species shares some traits with the new form, making necessary comparisons between the two.

Finally, we compare the morphology of the Peleng species with *R. feliceus,* a large-bodied and short-tailed endemic of Pulau Seram in the Malukus to the east of Kepulauan Banggai and Kepulauan Sula. *Rattus feliceus* resembles the Peleng rat in body size, certain external proportions, and fur coloration; it represents the most eastern occurrence of any species now placed in the genus *Rattus* that bears any resemblance to the new species endemic to Pulau Peleng.

Rattus koopmani, new species

HOLOTYPE: AMNH 109203, a young adult female collected by J. J. Menden (original number 65) from Pulau Peleng on July 15, 1938. The skin is slightly overstuffed, but its condition is good (fig. 32). The cranium is complete except for a missing right jugal, the dentaries are intact, and all teeth are present (figs. 11, 33). Measurements of the holotype are listed in table 14.

KNOWN DISTRIBUTION: Pulau Peleng (1°23′S, 123°14′E), the largest of the islands in Kepulauan Banggai, is separated from mainland Sulawesi by the deepwater Selat Peleng (fig. 4). The highest elevation of the island is about 1200 m. We have not been able to locate any specific locale or elevation where the specimen was collected, but we suspect it came from the lowlands because on the tag is written "ebene" (plain), which was Menden's designation for coastal lowland.

ETYMOLOGY: This species is named for Dr. Karl F. Koopman, Curator Emeritus in the Department of Mammalogy at the American Museum of Natural History.

DIAGNOSIS: Large body size, scantily haired tail that is shorter than length of head and body, dark brownish buff upperparts, grayish buff venter, thin and slightly harsh fur, small and dark ears, brown feet, five pairs of mammae, chunky skull, large teeth set in nearly parallel rows, a ridgelike posterior cingulum on the first molar, no cusp t3 on second and third molars, no anterocentral cusp on first lower molar, and small bulla relative to size of cranium distinguish *R. koopmani* from samples of any other known species of *Rattus.*

DESCRIPTION OF HOLOTYPE AND COMPARISON WITH *R. HOFFMANNI*: *Rattus koopmani* is a large, dark rat with a short tail (table 14). Fur covering the upperparts of the head and body is moderately dense; somewhat harsh to the touch; and composed of underfur, overfur, soft spines, and guard hairs. Underfur hairs are delicate and pale gray; overfur hairs have gray bases and are either tipped with brownish buff or with alternate bands of brownish buff and black. The flattened spinous hairs are about as long as the overfur (up to 20 mm) and are thin and flexible; al-

Fig. 32. Stuffed skin of the holotype (AMNH 109203) of *Rattus koopmani*. Measurements are listed in table 14.

though most are translucent, some are tipped with grayish black. Guard hairs are black for almost their entire lengths and are conspicuous even though they extend only 10–15 mm beyond the overhairs. Overall color of the dorsal coat is a burnished, dark brownish buff, darkest over the top of the head and back and paler along the sides.

The ventral coat is shorter (up to 10 mm thick) and softer than the dorsal pelage; short, translucent, and flexible spinous hairs occur throughout. The abdomen and inguinal region are dark gray tinged with buff. The chin, throat, and chest are stained brownish red.

The coloration of both the dorsal and ventral coats is similar to the pelage in samples of *R. hoffmanni*; the resemblance between *R. koopmani* and some specimens of *R. hoffmanni* from lowlands is very close. Fur texture, however, is different: *R. hoffmanni* has soft pelage, unlike the coarse texture characteristic of *R. koopmani.*

The mystacial, submental, superciliary, genal, and interramal vibrissae on *R. koopmani* resemble those of *R. hoffmanni* in length relative to size of head as well as in color. Ears are small relative to the overall size of the rat (about 9% of head and body length), are brownish black, are covered with short dark brown hairs on inside and outside surfaces, and are not sharply set off from the pelage color. These chromatic features are also similar to *R. hoffmanni,* but that species has relatively larger ears (13% of head and body length; fig. 34).

The dorsal surfaces of the front feet, from wrist to base of digits, are dark brown; digits and palmar surfaces are unpigmented. The naked palmar surface of each foot consists mostly of large interdigital pads and two larger metacarpal mounds. A silvery tuft of hair springs from the base of each cream-colored claw. Unpigmented ulnar carpal vibrissae form a conspicuous tuft just above each wrist.

The long and slender hind feet are dark brown everywhere; claws are cream and partially covered by brown and silvery tufts of hairs; plantar surfaces are naked. Interdigital pads 1 and 4 are posterior to pads 2 and 3, the thenar pad is thick and elongated, and the hypothenar is large and oval; smaller mounds occur at the posterior margins of some interdigital pads. Size relative to plan-

tar surface and shape and position of the plantar pads are similar to the morphology characteristic of *R. hoffmanni* (fig. 9).

The tail is conspicuously shorter than the combined lengths of head and body. It is dark brown everywhere, covered with circles of scales (12 per centimeter, counted about one-third the distance from the base), with three hairs at the base of each scale. The hairs are stiff and shorter than the length of the scales, so the tail appears hairless unless examined with a hand lens or microscope. *Rattus hoffmanni* also has a relatively short, brown tail, but it is longer relative to the length of head and body than that of *R. koopmani* (fig. 34), and because the hairs at the base of each epidermal scale are longer relative to scale length, the tail appears finely haired rather than nearly naked.

There are indications of 10 teats on the holotype of *R. koopmani*: a pectoral pair, postaxillary and abdominal pairs, and two inguinal pairs. Some teats were removed when the rat was skinned, and their former location is marked by a hole surrounded by concentric ridges in the skin. Judging by the size of the dry teats that remain, the animal was probably not lactating at the time it was captured. Four pairs of mammae are characteristic of *R. hoffmanni*; a pectoral pair is absent from nearly all specimens we examined.

The general conformation of the cranium and dentaries of *R. koopmani,* along with details of their bony anatomy, resembles the skull morphology common to samples of *R. hoffmanni* (contrast the views in figs. 10 and 11). Size (table 14) and certain proportions (fig. 34) are clearly the primary distinctions between the two species; the markedly larger cranium and mandible of *R. koopmani* are unmatched by any specimen of *R. hoffmanni* that we have examined. There are, however, additional differences other than size. The anterior zygomatic plate of *R. koopmani* does not project as far forward as it does in most specimens of *R. hoffmanni,* and therefore does not conceal the lateral nasolacrimal wall. That the zygomatic spine covers hardly any of the capsule is not a reflection of a longer rostrum, for in relation to skull length the rostrum is nearly the same length in each species. The posteroventral base of the zygomatic plate of *R. koopmani* is not as thick and sturdy, and meets the toothrow at about the level of the front of the first upper molar; the plate is thicker and wider in *R. hoffmanni,* so that the posteroventral margin is nearly even with the end of the first molar. *Rattus koopmani* has broader, more spacious incisive foramina than do most specimens of *R. hoffmanni*; the upper molar rows are nearly parallel rather than strongly diverging posteriorly; the bony palate is longer (relative to skull length); and the bullae are not as inflated (values for the ratio length of bulla divided by greatest length of skull are 14% in the holotype of *R. koopmani,* compared with 16%, the mean of a sample of *R. hoffmanni* from northeastern Sulawesi). The condyloid process of the dentary is more slender in *R. koopmani* than in *R. hoffmanni,* but all the other observed mandibular differences between the two species seem related to size.

Proportional contrasts between the two species are illustrated by the ratio diagram in figure 34. Compared with the sample of *R. hoffmanni,* the holotype of *R. koopmani* has a wider interorbit, mesopterygoid fossa, and bony palate at the level of the first molars, relative to zygomatic breadth; wider incisive foramina relative to their lengths; much smaller auditory bullae relative to greatest length of skull; and longer incisive foramina, diastema, and bony palate, relative to skull length. Other relative differences can be extracted from the graph.

Incisors and molars of *R. koopmani* are larger than those of *R. hoffmanni,* and molars are narrower (indexed by breadth of each first upper molar) relative to toothrow length (fig. 34), but in all other aspects of dental morphology the two species are much alike. Incisor enamel in *R. koopmani,* for example, is orange, and the upper incisors are opisthodont in configuration. The general occlusal patterns of the molars are similar in the two species (figs. 14, 16). *Rattus koopmani* has a ridgelike projection at the back of the first upper molar that we interpret to be a posterior cingulum. A projection and low ridge also define the posterior rim of the second upper molar, and the structure resembles a posterior cingulum much reduced in bulk over that seen on the first molar; most specimens of *R. hoffmanni* lack this conformation—a posterior cingulum is clearly absent from the

TABLE 14

Measurements (in millimeters) of Adult *Rattus hoffmanni, Rattus rattus, Rattus koopmani,* and *Rattus elaphinus*

(Mean ± SD, range [in parentheses], and sample size are given for each measurement)

	R. hoffmanni **NE Sulawesi**[a]	*R. rattus* **Pulau Peleng**	*R. koopmani* **Pulau Peleng**[b]	*R. elaphinus* **Pulau Taliabu**
LHB	170.1 ± 12.08 (144–200) 43	235.1 ± 10.9 (216–259) 21	233	192.1 ± 14.00 (168–215) 19
LT	169.5 ± 12.91 (150–192) 42	213.2 ± 19.32 (178–249) 20	215	170.0 ± 6.86 (154–180) 17
LHF	38.2 ± 1.44 (35–41) 59	42.2 ± 1.40 (40–45) 21	45	36.5 ± 1.02 (35–38) 19
LE	22.1 ± 2.31 (20–25) 20	24.3 ± 1.2 (21–27) 21	23	20.1 ± 1.05 (17–22) 19
TSR/cm	10.6 ± 1.00 (9–12) 17	9.6 ± 0.87 (8–11) 21	12	10.3 ± 2.35 (9–12) 19
GLS	42.5 ± 1.82 (37.7–46.1) 45	48.8 ± 1.42 (46.7–51.0) 20	52.5	44.4 ± 2.11 (41.5–48.7) 18
ZB	20.6 ± 0.87 (18.9–22.4) 47	22.3 ± 1.25 (20.1–24.2) 19	24.4	21.1 ± 1.38 (20.2–22.0) 19
IB	5.9 ± 0.28 (5.3–6.9) 60	6.9 ± 0.41 (6.3–7.6) 21	7.9	7.2 ± 0.43 (6.6–8.0) 19
LR	13.5 ± 0.77 (11.6–15.3) 60	15.8 ± 0.81 (14.4–16.9) 20	16.5	14.3 ± 1.01 (12.5–16.0) 17
BR	7.6 ± 0.40 (6.7–8.4) 56	9.0 ± 6.1 (8.1–9.8) 20	9.8	8.6 ± 0.65 (7.7–9.9) 19
BBC	16.5 ± 0.41 (15.5–17.5) 56	17.1 ± 0.52 (16.3–8.0) 21	18.7	16.7 ± 0.56 (16.1–18.4) 19
HBC	11.7 ± 0.49 (10.8–13.2) 46	12.5 ± 0.81 (11.4–14.3) 21	13.8	11.8 ± 0.52 (11.0–12.9) 19
BZP	4.8 ± 0.40 (4.0–5.8) 58	5.9 ± 0.41 (5.2–6.7) 21	5.5	5.1 ± 0.51 (4.2–5.9) 19
LD	11.1 ± 0.77 (9.3–12.4) 60	13.2 ± 0.82 (12.1–14.7) 20	14.3	12.0 ± 1.02 (9.7–13.9) 19
PPL	14.0 ± 0.83 (12.2–15.9) 16	17.9 ± 0.78 (16.1–19.0) 22	17.5	13.9 ± 0.79 (12.9–15.4) 21
LBP	8.4 ± 0.44 (7.0–9.4) 59	9.6 ± 0.47 (9.1–10.6) 21	11.7	9.6 ± 0.56 (8.7–10.6) 19
BBPM1	3.8 ± 0.40 (3.1–4.5) 44	4.6 ± 0.36 (3.9–5.1) 21	5.6	4.5 ± 0.28 (4.1–5.1) 19
EBPM3	1.2 ± 0.29 (0.7–1.8) 24	2.2 ± 0.41 (1.4–3.3) 22	2.6	2.3 ± 0.53 (2.0–3.3) 21
LIF	8.0 ± 0.52 (6.9–9.3) 60	9.6 ± 0.55 (8.8–10.4) 20	10.1	8.2 ± 0.54 (7.1–9.2) 19
BIF	2.8 ± 0.27 (2.0–3.6) 60	3.1 ± 0.30 (2.7–3.7) 20	3.9	3.2 ± 0.23 (2.8–3.6) 19
BMF	2.9 ± 0.26 (2.4–3.5) 43	3.0 ± 0.22 (2.6–3.5) 20	3.9	3.2 ± 0.19 (3.0–3.8) 19

TABLE 14—(*Continued*)

	R. hoffmanni NE Sulawesi[a]	*R. rattus* Pulau Peleng	*R. koopmani* Pulau Peleng[b]	*R. elaphinus* Pulau Taliabu
LB	6.9 ± 0.40 (6.0–7.7) 54	7.8 ± 0.35 (7.1–8.6) 24	7.2	6.4 ± 0.38 (5.7–7.1) 19
CLM1–3	7.3 ± 0.34 (6.4–7.7) 24	7.5 ± 0.20 (7.1–8.0) 18	8.7	6.9 ± 0.19 (6.5–7.1) 17
BM1	2.3 ± 0.12 (2.1–2.6) 60	2.3 ± 0.09 (2.1–2.4) 21	2.6	2.2 ± 0.11 (2.0–2.4) 16

[a] Localities 1, 9, and 14 (see fig. 6 and gazetteer).
[b] The holotype, AMNH 109203.

second molar. As in the configuration in *R. hoffmanni,* the anterolabial margins of the second and third molars of *R. koopmani* are defined by cingular ridges that support low bumps, but not discrete cusps that could be identified as cusp t3. There is no anterocentral cusp at the front of the first lower molar, and the full array of labial cusplets occurs on all three lower molars, as in *R. hoffmanni.*

We detect a few differences in occlusal pattern between the holotype and samples of *R. hoffmanni.* In *R. koopmani,* the laminae of the upper molars are not as straight as those of *R. hoffmanni,* especially the second lamina of the first molar and the front lamina of the second molar; the anterior lamina that forms most of the occlusal surface of the third upper molar is nearly C-shaped, a contrast to the less distorted and arcuate anterior lamina of the third molar in samples of *R. hoffmanni* (fig. 14).

The differences we see between the holotype of *R. koopmani* and our samples of *R. hoffmanni* are real, but just one specimen from Pulau Peleng is clearly an inadequate sample from which to obtain a realistic estimate of the range of morphological variation in this insular population. Some contrasts between the two species such as body size, pelage texture, and tail pilosity are impressive, but the other cranial, mandibular, and dental distinctions noted are few and some are subtle, amenable more to qualitative observation than quantitative analysis, and they will have to be tested if a large sample of *R. koopmani* is ever collected and studied.

NATURAL HISTORY: The habitat in which *R. koopmani* lives, its horizontal and altitudinal distribution in forests on the island of Peleng, and other aspects of its natural history are unknown. A short tail relative to length of head and body, combined with long and slender hind feet, suggests a terrestrial ecology.

COMPARISONS WITH OTHER *RATTUS* FROM PULAU PELENG

Our comparisons begin by contrasting *R. koopmani* with samples of two other Peleng *Rattus*—*R. exulans* and *R. rattus*—that are not endemic to the island. Then we compare *R. koopmani* with the native *R. pelurus.*

Rattus exulans: Although probably common in certain habitats on Pulau Peleng, few specimens of *R. exulans* from the island have been preserved as museum specimens. We have seen only two (MZB 4756, SMT 11338), but in features of skin, skull, and dentition, they are typical examples of the species found in that part of the world east of Borneo and west of New Guinea. *Rattus exulans* and *R. koopmani* are clearly dissimilar. Nearly half the body size of *R. koopmani* (contrast the measurement data listed in tables 13 and 14), *R. exulans* also has a tail that is much longer than the head and body (the tail is shorter than body length in *R. koopmani*) and four pairs of mammae (versus five pairs in *R. koopmani*). In addition to size, cranial contrasts are evident by comparing skulls of the two species illustrated in figure 35.

Rattus rattus: Samples of the house rat occurring on Pulau Peleng were described by

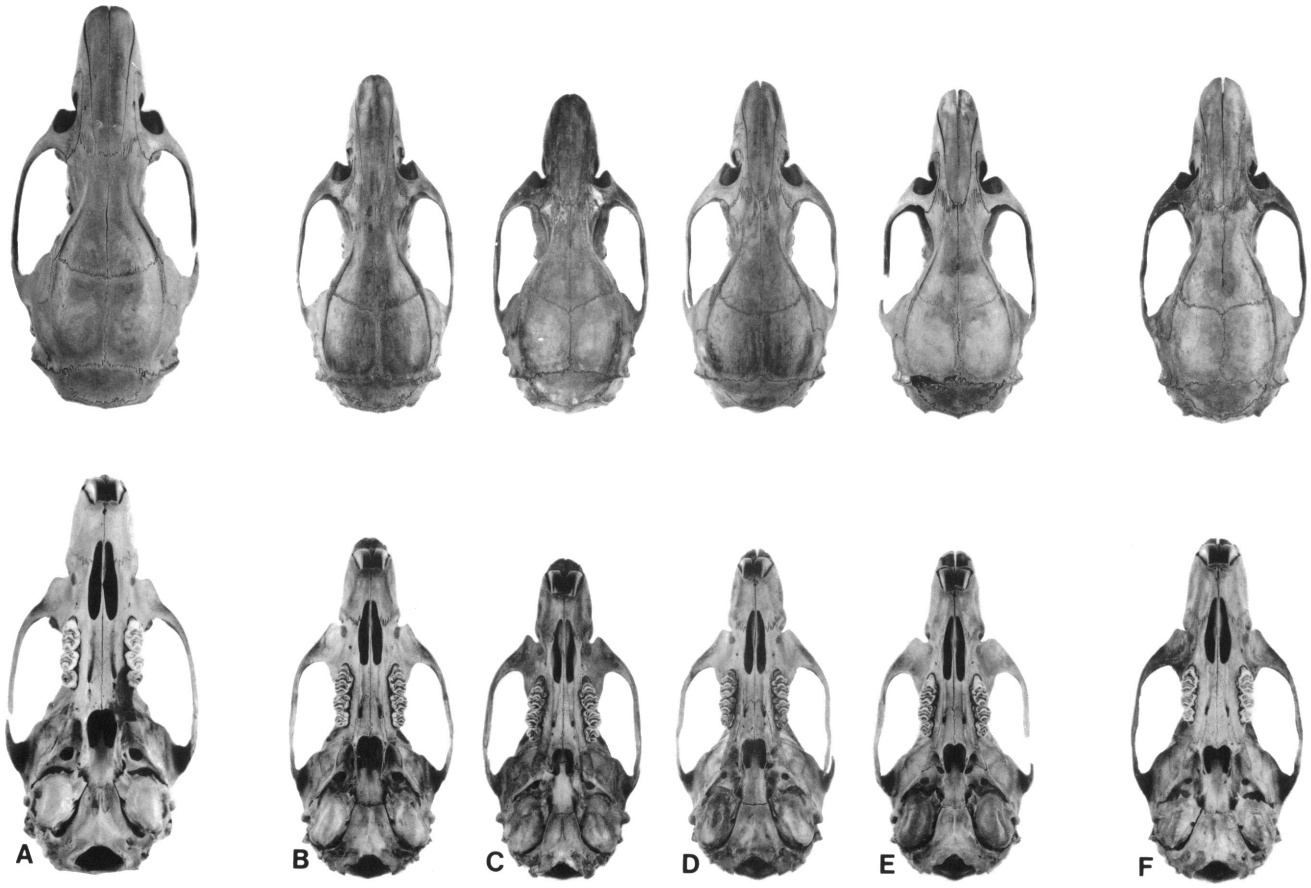


Fig. 33. Dorsal and ventral views (×1) of adult crania. The holotype of *Rattus koopmani* (**A,** AMNH 109203) is compared with representatives of *R. hoffmanni* from northern Sulawesi (**B,** USNM 216833), Gunung Klabat (**C,** USNM 217758), the central region (**D,** USNM 219583), and the southeastern peninsula (**E,** AMNH 101066), and with *R. elaphinus* (**F,** AMNH 109335) from Pulau Taliabu.

Sody (1941) as a well-defined subspecies, *R. rattus pelengensis.* We have examined 31 specimens of this form (AMNH 109179, 109185–109188, 109190–109200, 109202, 109204–109207, 109209–109211; MZB 4178–4184). Features associated with skins and skulls (which are the only kinds of preserved materials available for study) are like those that characterize the house rats found in most regions of Sulawesi. The primary distinction between rats on the two islands is size: *pelengensis* averages larger in body size than any sample of house rat from Sulawesi (compare the measurements of *pelengensis* in table 14 with those from samples of *R. rattus* from northern Sulawesi and Pulau Malenge, which are listed in table 12).

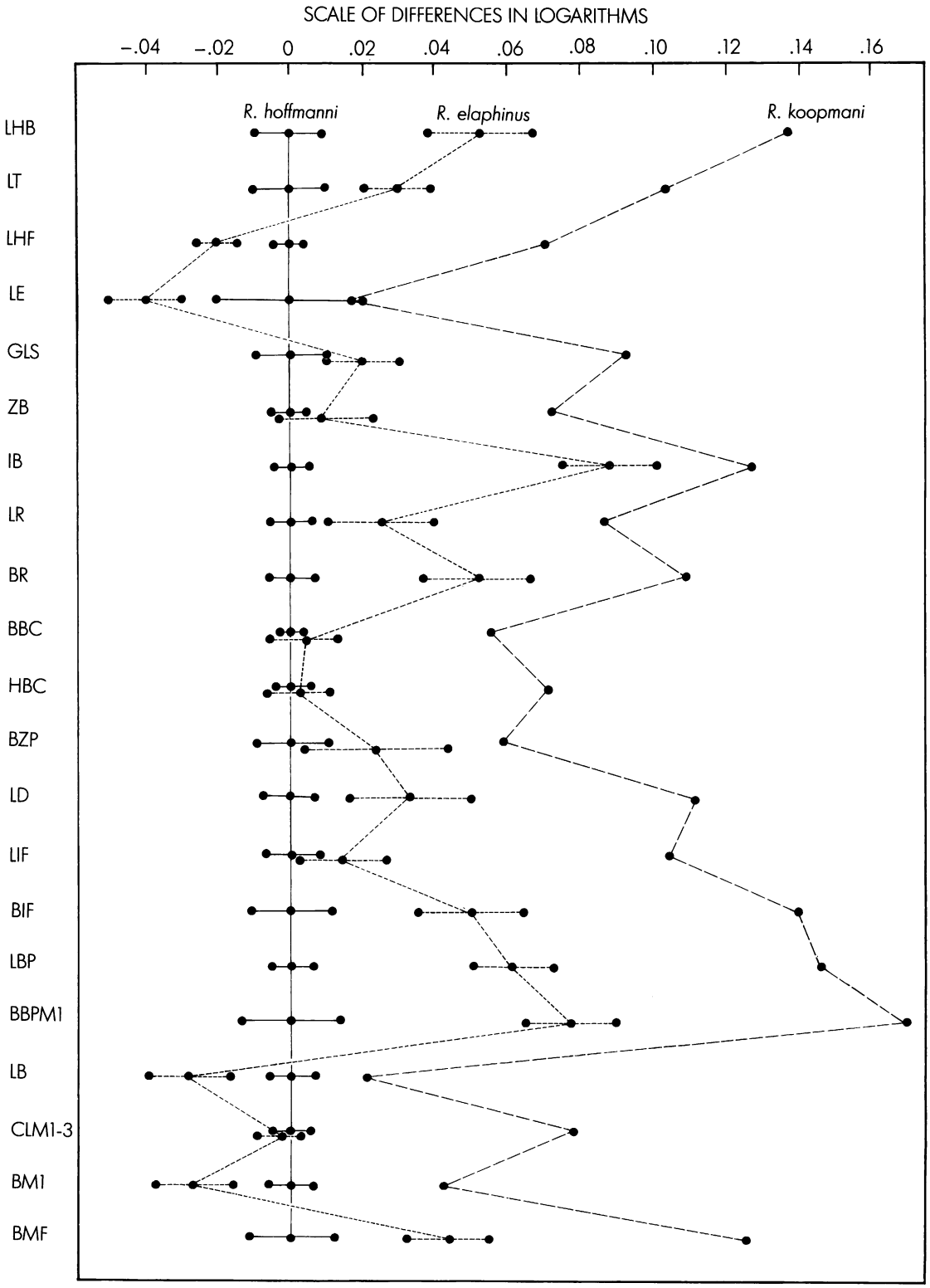
Unlike the relationship between *R. koopmani* and *R. exulans,* body size is more nearly comparable in *R. koopmani* and *R. r. pelengensis,* to the point that the holotype of *R. koopmani* had originally been cataloged in the American Museum as part of the series of *R. r. pelengensis.* But even though a close correspondence in size exists between the two species, the skull of the holotype is larger than that of any specimen of *R. r. pelengensis* we have seen, even the very oldest individuals, which mark the maximum values for the ranges of measurements listed in table 14. In addition to the difference in body size, *R. r. pelengensis* has paler fur (buffy brown or tawny upperparts, gray to buffy gray underparts), larger ears relative to body size, and longer guard hairs that project well beyond the overfur covering back and rump (compared with short, inconspicuous guard hairs in *R. koopmani*).

The relationship between *R. koopmani* and *R. r. pelengensis* in body size is reflected by the crania shown in figure 35; the greater dimensions of *R. koopmani* are clearly evident. Other distinctions between the two species can be seen: compared with *R. r. pelengensis,* the holotype has lower interorbital and postorbital ridges relative to cranial size, the sides of the braincase slope from temporal ridges to zygomatic roots (nearly vertical in *pelengensis*), incisive foramina are wider and more flaring in their posterior half, auditory bullae are not only much smaller in absolute values but especially relative to skull length, and toothrows are longer and the molars wider. The characters of *R. r. pelengensis* and the diagnostic features of the holotype of *R. koopmani* clearly index different kinds of rats, two species that are probably not even very closely related within a phylogenetic context.

Rattus pelurus: Originally described as *Rattus foramineus pelurus* by Sody in 1941 (p. 308), *R. pelurus* is an insular relative of species in the *R. xanthurus* group, which are endemic to mainland Sulawesi. A systematic revision of that group and its possible phylogenetic relationship to other species of *Rattus* will be published elsewhere (Musser and Holden, in prep.); a complete description of *pelurus* will be provided in that report, along with a discussion of its relationship to other species in the *R. xanthurus* group. We point out here only that *R. pelurus* and *R. koopmani* are strikingly dissimilar in morphology. *Rattus pelurus* is characterized by a much larger body size than *R. koopmani* (mean and range in length of head and body are 250.8 mm, 236–267 mm, 8 specimens; contrasted with 233 mm for the holotype of *R. koopmani*), a very long and partially bicolored tail (mean and range for a sample of 8 are 268.0 mm, 245–297 mm; short, monocolored tail in *R. koopmani,* table 14), wider hind feet with relatively larger palmar and plantar pads, larger and much paler ears, coarser fur, extremely long guard hairs (up to 60 mm, as opposed to about 35 mm in *R. koopmani*), grayish brown upperparts, and gray underparts. In chromatic and textural features of the fur, ears, and tail, as well as in absolute and relative lengths of appendages, *R. pelurus* stands in stark contrast to *R. koopmani.*

Sharp differences between the two species are also mirrored by cranial and dental characters (fig. 35). Compared with the holotype of *R. koopmani, R. pelurus* has a larger skull, shorter rostrum relative to dimensions of the braincase, shallower zygomatic notches reflecting much narrower zygomatic plates, shorter incisive foramina that usually do not project between the first molars, shorter bony palate that barely extends past the back margins of the third molars, larger and more inflated auditory bullae, and wider molars with more complex occlusal patterns.

Rattus pelurus and *R. koopmani* are easily distinguished by external features alone, and there is no evidence from either external, cra-


SCALE OF DIFFERENCES IN LOGARITHMS
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0
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.12
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R. hoffmanni
R. elaphinus
R. koopmani
LHB
LT
LHF
LE
GLS
ZB
IB
LR
BR
BBC
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BZP
LD
LIF
BIF
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LB
CLM1-3
BM1
BMF

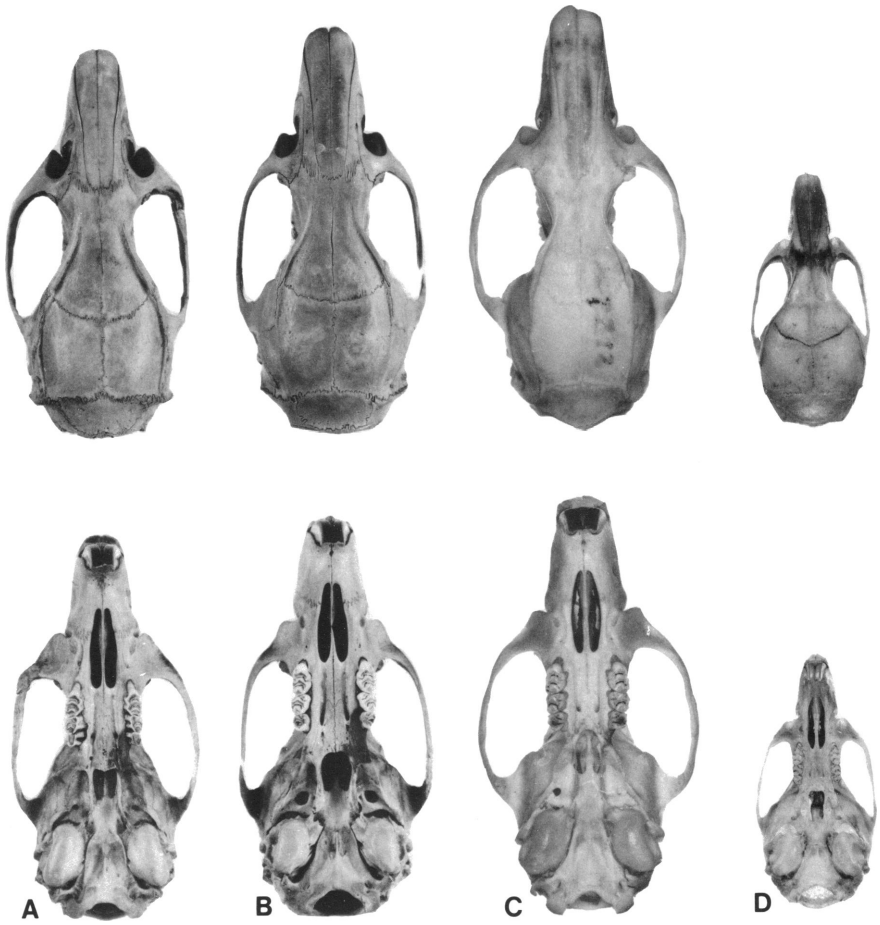

Fig. 35. Dorsal and ventral views (×1) of crania. The holotype of *Rattus koopmani* (**B,** AMNH 109203) is contrasted with three other species found on Pulau Peleng: *R. rattus pelengensis* (**A,** AMNH 109206), Peleng; *R. pelurus* (**C,** AMNH 109212), Peleng; and *R. exulans* (**D,** AMNH 215290), central Sulawesi.

nial, or dental morphology indicating them to be very closely related to each other.

The two species may be ecologically separated on Pulau Peleng. *Rattus koopmani,* as we suggested previously, is likely terrestrial in habitus. *Rattus pelurus* possesses a combination of characters—very long tail relative to head and body length, large ears, long guard hairs that project far beyond the overfur on back and rump, wide hind feet with prominent plantar pads, short and recurved claws, short rostrum, narrow zygomatic plates, and large auditory bullae—also shared by *R. xanthurus* and *R. marmosurus* from the mainland of Sulawesi. These features point to an arboreal lifestyle. Those two mainland species nest among roots of tall fig trees and beneath clumps of bamboo, but forage above the ground at levels ranging from crowns of understory trees up into the canopy (Musser, personal obs.). The morphology of *R. pelurus* strongly suggests a similar ecology.

←

Fig. 34. Ratio diagram. Dimensions are compared among samples of *Rattus hoffmanni* (the standard), *R. elaphinus,* and *R. koopmani.*

Comparisons with *Rattus elaphinus*

Rattus elaphinus is indigenous to Palau Taliabu in Kepulauan Sula, the archipelago just east of Pulau Peleng. It is the only species from Taliabu to have been described in the taxonomic literature; its morphology and geographic proximity to Pulau Peleng require that it be contrasted with *R. koopmani.*

We provided a description of *R. elaphinus* in the previous section when we compared it with samples of *R. hoffmanni.* These two species, although superficially alike, differ in a suite of qualitative and proportional features. In many respects, *R. elaphinus* is more like *R. koopmani* than any other species of *Rattus.* Except for its coarser and darker fur, much greater body size (table 14), and different mammary count (four pairs in *R. elaphinus,* five pairs in *R. koopmani*), the holotype of *R. koopmani* matches the sample of *R. elaphinus* in proportional relationships of external and dental dimensions (fig. 34) and in general conformation of the cranium (fig. 33); cranially, *R. elaphinus* is very much a small version of *R. koopmani,* at least as that species is represented by the holotype. Whether the proportional similarities between the Peleng and Taliabu species point to close phylogenetic relationships, morphological convergence, or parallelism is difficult to evaluate without study of other anatomical systems as well as more examples of *R. koopmani.* At least one of the proportional features linking the two species—the small auditory bullae relative to length of skull—is a primitive character in murid rodents (Musser and Newcomb, 1983). Although the two species are similar in proportions, our comparisons indicate that in its greater size, very different pelage, and higher number of mammae, the holotype from Pulau Peleng represents a species morphologically distinct from *R. elaphinus.*

Comparisons with *Rattus feliceus* from Seram

Described by Oldfield Thomas in 1920 (p. 423), *R. feliceus* is known from the holotype (BM 20.7.26.7) and four other specimens (BM 20.7.26.4, 20.7.26.5, 20.7.26.6, 20.7.26.8) collected on the Moluccan island of Seram by Charles, Felix, and Joseph Pratt during January and February 1920. Four of the rats were taken from 4600 and 6000 ft on the slopes of Gunung Manusela, and one was collected at sea level near Teluk Taluti (Teloeti Bay), South Seram. All were "trapped in heavy jungle in precipitous limestone country," according to notes on labels attached to the study skins.

Thomas thought *feliceus* to be a distinctive species, and though he compared some of its characters with *R. mordax, R. leucopus, R. ringens,* and *R. ratticolor,* a suite of species forming part of the native New Guinea fauna, he also noted that *R. feliceus* "is easily distinguishable by its much greater size, reddish colour, and white belly from *R. mordax,* which alone of this group of Papuan species has its mammary formula" (p. 424). Between 1920 and the middle 1930s, the status of *feliceus* as a species was not questioned; in 1936, for example, Tate delineated a "*Rattus ringens* group," which to him formed "a characteristic and integral part of the fauna of New Guinea" (p. 543) and declared that a "further member of the same assemblage is probably to be seen in *feliceus* of Ceram" (p. 545). By 1938, and from then up to 1986, *feliceus* fell to the level of subspecies and was associated with other species of *Rattus.* In 1938, Rummler asserted emphatically that the Seram animal was nothing more than a member of the *leucopus* group and regarded *feliceus* to be but a subspecies of *Stenomys leucopus,* thus representing on Seram a species that in Rummler's view was otherwise indigenous to New Guinea and parts of Australia. Several years later, Ellerman (1941: 205) also listed *feliceus* as a subspecies of *leucopus* (calling it *Rattus leucopus* because he did not recognize *Stenomys* as a genus), but changed his mind in 1949 (p. 69) and attached *feliceus* to *R. ringens* as a subspecies. In the last checklist in which *feliceus* is entered, Laurie and Hill (1954) used the name *R. ruber* to embrace the New Guinea *ringens* and *leucopus* and listed the Seram rat as a subspecies of *R. ruber.* Not one of these taxonomic allocations of *feliceus* was documented, and we know of no data in the literature supporting the identity of *feliceus* as a subspecies of any kind of *Rattus.*

Most of the New Guinea species of indigenous *Rattus* are not closely related to *R. feliceus*. In their systematic revision of *Rattus* in the New Guinea region, Taylor et al. (1982) pointed out that the holotype of *ruber* is an example of the introduced *R. nitidus* and that previous to their study the name had been applied to specimens of five species of *Rattus* (*praetor, steini, jobiensis, giluwensis,* and *mordax*); they recognized *R. leucopus* as part of the New Guinea murid fauna and *ringens* as a distinctive subspecies of *R. leucopus*. The morphological and geographical boundaries of the subspecies of *R. leucopus,* as described by Taylor et al., do not overlap and do not include either the morphology of *feliceus* or its insular range. Our first-hand study of large samples of Australian and New Guinean *R. leucopus* indicates also that the Seram animal is not the Moluccan counterpart of *R. leucopus,* is not particularly closely related to it, and cannot be morphologically closely linked as a subspecies (or island population) to any other species of *Rattus* native to the New Guinea region. Future analyses may demonstrate *feliceus* to be phylogenetically closer to species in the New Guinea fauna than to other assemblages of *Rattus* found to the west and south of the Moluccas, but whatever the pattern of relationship that may emerge, to us, the characters defining *feliceus* mark a distinctive species known only from Seram. In their world list, Corbet and Hill (1986: 194) also recognized *feliceus* as a species of *Rattus*.

Thomas (1920: 423) characterized *R. feliceus* as a "large spinous-haired species with 2-2=8 mammae and a short, nearly naked, scaly tail." He went on to describe it as being large in body size,

> Fur long, profusely mixed with spines, both hairs and spines on back about 20 mm. in length, and the latter about 0.5 in breadth. General colour above deep rich rufous-brown, grizzled with blackish, the hairs slaty with rich rufous tips; the longer bristle-hairs on the posterior back with buffy tips. Sides clearer rufous. Under surface white, not very sharply defined laterally, the hairs white to their bases. Head browner and less rufous than back. Ears comparatively short, blackish brown. Hands and feet very thinly haired, flesh-coloured, the fine hairs whitish. Tail not as long as the body without the head, almost naked, the scales very large (about six rings to the cm.), uniformly pale brown.

The skull, wrote Thomas, was large, the "Zygomatic well thrown out anteriorly. Supraorbital beads well developed, passing backwards to the middle of the parietals, but not forming postorbital processes. Palatine foramina large and well open, their hinder edge level with the front root of m^1. Choanal opening broad, some way behind molars. Bullae of medium size. Incisors somewhat opisthodont. . . . Molars as usual."

Rattus koopmani and *R. feliceus* are superficially similar in some external features. Both are large rats with coarse fur, and in each the tail is shorter than length of head and body. With these characters, the similarity ends. Aspects of the pelage and morphological characteristics of the skin that distinguish the two species are listed in table 15, external measurements in table 16.

The cranium of *R. koopmani* is compared with a young adult and an old adult of *R. feliceus* in figures 36 and 37; cranial and dental measurements are listed in table 16. Compared with examples of *R. feliceus* of about the same body size, the cranium of *R. koopmani* is slightly larger and in dorsal view appears more massive and less angular. The distance across the zygomatic arches is greater in *R. koopmani,* the interorbit wider, and the rostrum wider and shorter relative to skull length, giving it a chunky aspect compared to the longer and more slender rostrum characteristic of *R. feliceus*. The zygomatic plates are about equally broad in the two species, but the zygomatic notch is deeper in *R. koopmani,* indicating a more forward projection of the anterior spine of each plate.

Seen in ventral view, crania of the two species resemble one another in size and general conformation as well as toothrow length and molar breadth. Compared with young adult *R. feliceus, R. koopmani* has a longer diastema, wider incisive foramina, narrower mesopterygoid fossa, and larger bulla—not only in absolute value but also relative to the size of the cranium. Finally, the molar rows are nearly parallel in *R. koopmani,* but they diverge posteriorly in *R. feliceus*.

Dentaries of the two species are similar in outline and topography, but differ in details. Those of *R. koopmani* are longer, are deeper through the ascending ramus, and have higher and more robust coronoid processes (fig. 37).

TABLE 15

Contrasts between Adult *Rattus koopmani* and *Rattus feliceus* in External and Chromatic Traits

Trait	*R. koopmani*	*R. feliceus*
Upperparts	Brown, similar to *R. hoffmanni*; fur shorter and softer, with fewer semirigid spines; guard hairs black with pale bases	Brownish orange; fur longer (overhairs extend up to 30 mm along the back) and harsher, with many long, wide, and semirigid spines; guard hairs black with unpigmented bases and tips
Underparts	Chin, throat, and chest reddish brown; abdomen and inguinal areas dark gray tinged with buff	Chin, throat and chest white (hairs are white to their bases); abdomen and inguinal regions whitish gray
Feet	Dark brown	Now yellowish due to grease stain, but probably white in life; upper surfaces covered with short, silvery hairs
Tail	Actually longer (table 16) and longer relative to length of head and body; 12 rings of scales/cm; brownish black	Actually shorter (table 16) and shorter relative to length of head and body; scales are longer so there are fewer rings (6–8/cm in 5 specimens); pale brown
Ears	Brownish black	Pale brown
Mammae	10 (1 pectoral pair, 1 postaxillary pair, 1 abdominal pair, and 2 inguinal pairs)	8 (1 pectoral pair, 1 postaxillary pair, and 2 inguinal pairs)

Based on these samples, and admittedly they are small, we see no evidence from characters in skins and skulls to indicate a tight link between *R. koopmani* from Pulau Peleng and *R. feliceus* from Pulau Seram. The single specimen and the small series simply point to rats having large bodies, short tails, coarse pelage, and insular origins that seem otherwise not to be closely related, either morphologically or phylogenetically. Possibly the phylogenetic relationships of *R. feliceus* are with one or more of the species of *Rattus* found on New Guinea, a biogeographic link, as Dr. Colin P. Groves informed us, that parallels the one between the bandicoot *Rhynchomeles,* endemic to Seram, and the bandicoot *Echymipera,* native to New Guinea.

CONCLUDING OBSERVATIONS

Membership in *Rattus*

Do *hoffmanni, mollicomulus,* and *koopmani* belong in the genus *Rattus*? We pose this query because in 1941 Sody made *R. hoffmanni* the type species of the genus *Mollicomys,* and included *R. mollicomulus* in it. Lack of a pair of pectoral mammae and presence of four other pairs were the only features used by Sody to diagnose the genus. Until his action, *hoffmanni* had always been placed in either *Mus* or *Rattus.* The species was originally described as a variety, *celebensis,* of *Mus rattus* by Hoffmann in 1887. This arrangement was also used by Trouessart in 1897 (p. 477), when he listed the variety "*celebensis*" as form "*d*" under the species "*rattus*" in the section "*Epimys*" of the genus "*Mus*" in his catalog of living and fossil mammals. Because the name *celebensis* had earlier been used by Gray in 1867 to identify a different rat, Matschie in 1901 provided Hoffmann's taxon with the name *hoffmanni,* and regarded it not as a variety of *M. rattus* but as a distinct species of *Mus.* Probably influenced by Matschie, Trouessart (1904: 369) also listed *hoffmanni* as a species in a *Rattus* section under an *Epimys* group of the genus *Mus.* Years later, *Mus* came to be restricted in scope and the name *Epimys* to be replaced by *Rattus* (see Ellerman, 1941, for a history of these changes).

By the 1920s, *hoffmanni* was unquestionably linked to *Rattus* as a species (Miller and Hollister, 1921a; Raven, 1935), and until 1941 it was also untied from close association with house rats, *R. rattus.* Tate, in 1936 (p. 547), for example, considered the morphology of *hoffmanni* to be sufficiently distinctive from other species of *Rattus* that it formed the nucleus of his *R. hoffmanni* group, a clus-

TABLE 16

Sex, Age, and Measurements (in millimeters) of Specimens of *Rattus koopmani* and *Rattus feliceus*

		R. feliceus				
	R. koopmani: AMNH 109203	BM 20.7.26.5	BM 20.7.26.4	BM 20.7.26.7	BM 20.7.26.8	BM 20.7.26.6
Sex	Female	Male	Male	Female	Female	Female
Age	Young adult	Old adult	Young adult	Adult	Adult	Young adult
LHB	233	225	200	210	220	200
LT	195	185	175	172	180	165
LHF	45	46	46	45	46	44
LE	23	23	22	22	23	22
GLS	52.5	54.3	—	50.7	—	50.9
ZB	24.4	25.2	22.6	23.9	—	23.3
IB	7.9	7.4	7.2	7.1	7.7	6.7
LR	16.5	18.4	16.4	21.8	17.6	16.4
BR	9.8	10.0	9.3	9.5	10.4	8.9
BBC	18.7	19.5	—	18.8	—	18.1
HBC	13.8	14.0	—	14.0	—	13.8
BZP	5.5	6.5	5.6	5.5	5.8	5.7
DZN	3.4	1.9	2.0	2.1	2.5	1.7
LD	14.3	14.1	13.2	14.4	15.3	13.4
LIF	10.1	11.6	9.8	9.6	10.0	9.0
BIF	3.9	3.8	3.2	3.8	3.9	3.1
LBP	11.7	11.4	11.5	11.3	11.5	12.3
BBPM1	5.6	5.7	4.9	5.3	5.2	5.0
BBPM3	6.0	6.8	6.4	6.7	6.3	6.3
DT[a]	0.4	1.1	1.5	1.4	1.1	1.3
BMF	3.9	4.2	4.1	4.7	4.2	4.1
LB	7.2	6.8	—	6.6	—	6.5
CLM1–3	8.7	8.5	8.6	8.4	8.2	9.0
BM1	2.6	2.7	2.5	2.5	2.5	2.6

[a] Divergence of toothrows: the difference between breadths of bony palate at first and third molars.

ter that also contained *R. mollicomus* and *R. mollicomulus.* In addition, Tate listed *linduensis* and *subditivus* as subspecies of *R. hoffmanni.*

Ellerman, in 1941 (p. 184), also recognized a "*hoffmanni* group." He accepted Tate's contents of this cluster but to it added *Rattus palelae, R. pulliventer,* and *R. rogersi.* Ellerman (1941: 215) was unsure about the merit in recognizing the group, however, and wrote that

> *R. hoffmanni* seems very poorly differentiated from *rattus* Rats except by its broader molars, though regarded as the type of a separate group by Tate. Its mammary formula, I—3 = 8, turns up intermittently elsewhere, as in *R. bagopus,* from the Philippines, *R. rogersi* from the Andamans, etc. It suggests a direct derivative from the 2—3 = 10 formula often present in *rattus* Rats. In all other main characters, as skull, and colour of tail, it seems essentially like *rattus*-group Rats. However, the tail is most often shorter than the head and body in *hoffmanni,* which is not usual in *rattus* Rats, though sometimes occurring.

In the third volume of his checklist, Ellerman (1949: 61) continued to list *hoffmanni* as a species of *Rattus* and associated the names *mollicomus, mollicomulus,* and *palelae,* with a question, as subspecies of *R. hoffmanni,* commenting that he was unsure of the status of the three. This arrangement was the one adopted by Laurie and Hill (1954) in their list of the mammals of the Indo-Australian region. From that date to the present, *hoffmanni* has continued to be viewed as a species of *Rattus* (Misonne, 1969; Musser, 1987).

Our study has not revealed any characters of skin, skull, and teeth that could be used to exclude *hoffmanni* from *Rattus.* Specimens of *R. hoffmanni,* along with examples of *R.*

Fig. 36. Dorsal and ventral views (×1) of crania. The holotype of *Rattus koopmani* (**left,** AMNH 109203) is compared with young adult (**middle,** BM 20.7.26.6) and old adult (**right,** BM 20.7.26.5) examples of *R. feliceus.*

mollicomulus, exhibit a suite of morphological characters, which we accept as derived (see Musser and Newcomb, 1983), also shared by *R. rattus,* whether European or Asian forms are considered (the relationship, as well as the taxonomic problems involved, between the European house rat, which is native to the Indian Subcontinent, and the house rats native to Southeast Asia are discussed by Musser and Califia, 1982). These traits are briefly outlined below.

1. The hind feet are moderately long (fig. 9).

2. Ridges outline the postorbital region and dorsolateral sides of the braincase (fig. 10).

3. The interparietal is wide and deep (anterior–posterior dimension), roofs most of the occipital region, and either does not or barely projects anteriorly between the parietals (fig. 10).

4. In the orbit, the sphenopalatine foramen is far anterior to the dorsal palatine foramen (Musser and Newcomb, 1983: 344, fig. 8). On the ventral surface of the bony palate, the posterior palatine foramen is opposite the contact between second and third molars (figs. 10, 12B).

5. Squamosal roots of the zygomatic arches originate moderately low on the sides of the braincase (fig. 10).

6. Zygomatic plates are wide and have a

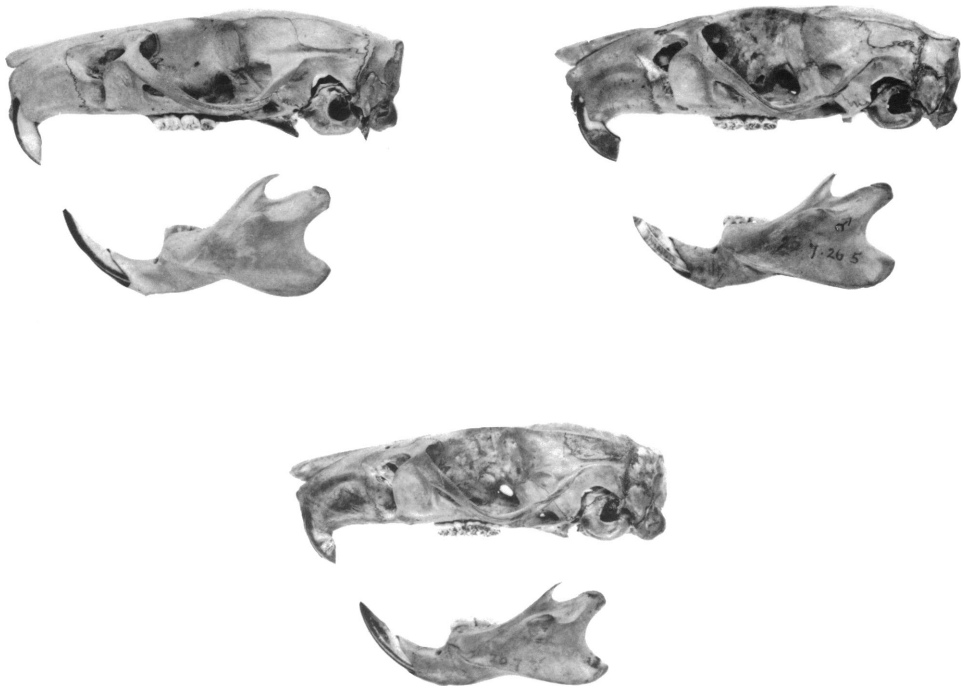

Fig. 37. Lateral views (×1) of crania and dentaries of same specimens illustrated in figure 36. *Rattus koopmani* (upper left) is compared with an old adult (upper right) and young adult (bottom) of *R. feliceus*.

strongly projecting anterior spine, which forms a well-defined zygomatic notch, as seen in dorsal view (fig. 10).

7. Large postglenoid foramina (fig. 12A) are confluent with wide middle lacerate foramina (fig. 12B), effectively separating the anterodorsal margins of the bullae from the braincase.

8. No alisphenoid strut covers the lateral portion of the alisphenoid canal, which is really an open channel (fig. 12A). Without the strut, the masticatory-buccinator foramina and the foramen ovale accessorius are united.

9. Long incisive foramina project between the anterior margins of the first molars (figs. 10, 12B).

10. The bony palate is wide and extends appreciably posterior to the molar rows as a wide, shelflike expansion (figs. 10, 12B).

11. The mesopterygoid fossa is narrow in relation to the width of the bony palate. Its walls are breached by spacious sphenopalatine vacuities that extend along each side of the basisphenoid and presphenoid far enough anteriorly to be seen in the back of the orbit (fig. 12).

12. Each pterygoid plate is wide and slants toward the medial sagittal plane of the cranium, forming a moderately deep fossa. Large sphenopterygoid vacuities perforate the plates, and each plate is margined by a prominent pterygoid ridge (fig. 12B).

13. Auditory bullae are round, large relative to the size of the cranium, and moderately inflated; each eustachian tube is short and wide (figs. 10, 12).

14. Molars have multiple roots: each first upper tooth is anchored by five roots, the second by four, and the third by three. Each first lower molar is secured by four roots, the second and third by three roots beneath each one (fig. 13).

15. In each upper toothrow, the first molar broadly overlaps the second, which overlaps the third. In each lower row, there is slight overlap of the third molar on the second, but broader overlap of the second on the first (figs. 14–16).

16. Primary cusps are not discrete, but broadly connected so that most merge in each row to form a weakly cuspidate lamina.

17. The rows of cusps on each upper and

lower molar are close to one another, separated by only a slight space (figs. 14, 16).

18. A posterior cingulum is absent from the back of each upper molar in specimens of most species. If present, it is not fixed, usually occurring in half or less of any sample, and is variable in shape, ranging from a slight triangular bulge to a small discrete cusp (fig. 15).

19. A cusp t3 on the second or third molars either does not occur or when it does is small (fig. 15).

20. First lower molars lack anterocentral cusps (fig. 16).

21. The karyotype has a 2N of 42, FN of 61 (males) and 62 (females), 7 pairs of metacentric chromosomes that grade in size from medium to small, no submetacentric pairs, and 11 pairs of telocentrics (fig. 17).

Other features are shared by *R. hoffmanni* and *R. rattus,* but they either are primitive and common to many species in other genera or are characters with, in our minds, uncertain or unknown polarities. Marked contrasts also exist between *R. hoffmanni* and not only *R. rattus* but all other described species in the genus, and these distinctions are embodied in our diagnosis of *hoffmanni.* The absence of a pectoral pair of mammae in nearly all samples of *R. hoffmanni* is one of those differences between that Sulawesian endemic and nearly all other species of *Rattus,* certainly those usually considered to be part of the subgenus *Rattus* (Ellerman, 1941, 1949), in which all the species have two pectoral teats connected to extensive mammary tissue (Musser and Newcomb, 1983). A very few specimens of *R. hoffmanni* have small pectoral teats unconnected by ducts to mammary tissue. That observation, in the context of the many derived traits shared by *R. hoffmanni* and *R. rattus* and its allies, suggests that the mammae count in the former resulted from loss of the pectoral mammary complex. To us, as well as Ellerman (1949: 190), this is simply an apomorphy that helps define the specific boundaries of *R. hoffmanni* and the limits of *R. mollicomulus* in relation to other species of *Rattus.* It is not a character signifying that *R. hoffmanni* should be placed in a monophyletic group other than *Rattus,* as Sody (1941) contended when he diagnosed the genus *Mollicomys* by number and position of mammae.

The single specimen of *R. koopmani* from Pulau Peleng has pectoral mammae, as do *R. rattus* and its relatives. Its bullae are less inflated and smaller relative to cranial size than are the auditory bullae in most species in the subgenus *Rattus,* which may reflect the retention of a primitive condition; otherwise, no morphological or chromatic features exist in the skin and skull of this specimen that point to the inclusion of *koopmani* in any other genus but *Rattus.*

Distributional Associations

The revision of species boundaries within the *Rattus hoffmanni* group and the discovery of a new species on Pulau Peleng alter the size of the murid fauna native to the Sulawesian region. Our current tabulation lists 48 species in 14 genera (table 17). Most of the species co-occur with *R. hoffmanni, R. mollicomulus,* and *R. koopmani* in different combinations.

Rattus koopmani and *R. pelurus* are the only two native rats so far collected on Pulau Peleng. We suspect they live together in the same primary forest, but we lack data from the field to substantiate that intuitive view. *Rattus rattus* and *R. exulans* are also recorded from the island, but are probably restricted to habitats associated with humans; that is certainly where they are found on mainland Sulawesi.

Rattus mollicomulus has been taken only on the upper slopes of Gunung Lompobatang in the southwestern arm of Sulawesi. Specimens of that rat have been collected at the same localities which yielded examples of *Rattus bontanus, Paruromys ursinus, Maxomys hellwaldii, M. musschenbroekii,* and *Lenomys meyeri.* The specimens of *R. mollicomulus* were probably trapped in the same forests as were the samples of these other species, for all were collected by Gerd Heinrich during one field trip in 1931; however, we lack confirming field information.

Depending on the altitude and forest formation, *R. hoffmanni* co-occurs with nearly all the endemic species recorded from Sulawesi, excluding those inhabiting Pulau Peleng

and populations of the species recorded from upper slopes of Gunung Lompobatang, where *R. hoffmanni* is replaced by *R. mollicomulus*. Trapping results from Guy Musser's work in central Sulawesi illustrate the syntopic spatial configurations of *R. hoffmanni* in relation to other species of native rats. Below we provide selected capture records of *R. hoffmanni* from the Kuala Navusu region in lowlands, Sungai Sadaunta at intermediate elevations, and Gunung Nokilalaki in the mountains.

KUALA NAVUSU (1975)—LOWLAND EVERGREEN RAIN FOREST

AMNH 226025 (100 ft; Sept. 2): Top of rotten trunk across wet ravine. *Maxomys hellwaldii* was caught in the same place.

AMNH 226026 (125 ft; Oct. 9): Caught 4 ft above a stream on rotten tree trunk extending from one stream terrace to the other. *Echiothrix leucura, Paruromys dominator,* and *Maxomys hellwaldii* were caught on the same trunk.

AMNH 226039 (400 ft; Oct. 9): In tangle of woody shrub and vine on the ground. *Rattus facetus* was trapped on woody vine in forest understory 12 ft above this spot.

AMNH 226041 (700 ft; Oct. 12): On damp ground sheltered by boulder and exposed tree roots. *Paruromys dominator* was trapped in the same spot.

AMNH 226035 (250 ft; Oct. 18): Taken on woody vine (¾ in. diameter) 6 ft above ground that is part of an extensive tangle of woody vines intertwined about one thick vine (5 in. diameter). The tangle extends over a steep hillside and is anchored by woody shrubs on the ground and tree crowns in the understory; the trap was placed on a vine leading off the main tangle; the rat could reach it from the ground by climbing the short woody shrubs or the larger vines in the tangle. *Maxomys hellwaldii* was trapped on a large vine near the ground 3 ft away from where the *R. hoffmanni* was caught; *Haeromys minahassae* was taken about 8 ft upslope and higher in the vine mass.

AMNH 226032 (150 ft; Nov. 4): Caught among large rocks that form streambank; rocks are covered with moss and are nearly hidden beneath thick cover of shrubs, rattan, and ferns. *Maxomys hellwaldii* and *Bunomys andrewsi* were trapped at the same site.

AMNH 226037 (300 ft; Nov. 19): Caught on large section of rotten tree trunk bridging steep, rocky, and mossy sides of a streambed. *Paruromys dominator* was caught in the same place.

SUNGAI SADAUNTA (1975)—LOWLAND EVERGREEN RAIN FOREST

AMNH 224983 (2600 ft; Sept. 24): Caught on wet ground at hollow end of rotten tree trunk on hillside. *Bunomys chrysocomus* was trapped at the same spot.

AMNH 224963 (2700 ft; Sept. 25): Caught on thin, woody vines that loop down from crowns (30–40 ft above ground) of understory trees; bottoms of loops, where trap was placed, are about 3 ft above ground. *Paruromys dominator* was taken in the same trap on a different day.

AMNH 224964 (2700 ft; Sept. 26): On top of wet, rotten, and mossy tree trunk across Sungai Sadaunta; here streambed is about 70 ft wide and trunk completely bridges stream just above its surface and rests partly on boulders in the water. *Maxomys hellwaldii* and *Taeromys celebensis* were caught on top of the same trunk.

AMNH 224973 (2850 ft; Oct. 7): In ground depression beneath base of large tree in forest undergrowth of rattan and dense shrubs. *Maxomys hellwaldii* was caught in the same place.

AMNH 224966 (2700 ft; Oct. 8): Trap on damp ground beneath splintered base of large tree that lay on stream terrace above Sungai Sadaunta. Now rotten and covered with moss, shrubs, ferns, and vines, the trunk provides covered spaces and paths under the area where it splintered from the stump, which is completely surrounded by dense shrubbery (up to 4 ft high), tall gingers, and rattan. *Paruromys dominator* and *Bunomys* sp. were trapped in the same spot; other examples of *P. dominator,* as well as *Bunomys chrysocomus, Maxomys hellwaldii,* and *Rattus facetus* were caught on the adjacent forested hillside just above this section of terrace.

AMNH 224971 (2800 ft; Sept. 28): Trap on long, wet, and rotten palm trunk (*Pigafetta* sp.) bridging Sungai Sadaunta about 5 ft above water level. *Maxomys* sp. B was caught on same trunk.

AMNH 224978 (2900 ft; Oct. 20): On wet runway alongside section of rotten and wet tree trunk covered with moss and epiphytes and concealed by shrubs and ferns; on a high terrace 15 ft above stream. *Echiothrix leucura* was caught below this terrace near the water's edge.

AMNH 224970 (2700 ft; Oct. 27): This rat, along with *Crunomys celebensis* and *Maxomys musschenbroekii,* was caught on the same section of tree trunk that is part of an old and rotten tree-fall laying across Sungai Sadaunta and connecting the level terraces along each side of the stream. Rocky and muddy, these terraces are not only covered by the sprawling tangle of tree-fall, but also by rotten palm trunks and fronds, all nearly hidden in thick shrubbery, ferns, and tall gingers. *Tae-*

TABLE 17

Species of Murid Rodents Indigenous to Sulawesi: Their Distributions in Different Regions of the Island, on Pulau Peleng, and within Forest Formations

(Most of the taxa are described in Musser [1981a, 1982b, 1991], in Musser and Newcomb [1983], in publications referenced in Musser [1984, 1987], or in the present report. Other species, as well as undescribed taxa, will be discussed in manuscripts being prepared for publication.)

	Region of Sulawesi					
Genus and species	North	Central	Southeast	Southwest	Pulau Peleng	Tropical rainforest formation[a]
Crunomys celebensis		+				Lowland evergreen
Echiothrix leucura	+	+				Lowland evergreen
Tateomys macrocercus		+				Upper montane
Tateomys rhinogradoides		+				Upper montane
Melasmothrix naso		+				Upper montane
New genus and species		+				Upper montane
Margaretamys beccarii	+	+				Lowland evergreen
Margaretamys elegans		+				Lower and upper montane
Margaretamys parvus		+				Lower and upper montane
Lenomys meyeri	+	+		+[b]		Lowland evergreen to upper montane
Lenomys sp.				+[c]		Lowland evergreen
Eropeplus canus		+				Lower and upper montane
Haeromys sp.		+				Lower and upper montane
Haeromys minahassae	+	+				Lowland evergreen
Maxomys musschenbroekii	+	+	+	+[b]		Lowland evergreen to upper montane
Maxomys dollmani		+	+			Lower montane
Maxomys hellwaldii	+	+	+	+[b]		Lowland evergreen
Maxomys sp. A		+				Lowland evergreen
Maxomys sp. B		+				Lowland evergreen to lower montane
Maxomys wattsi		+				Lower and upper montane
Bunomys chrysocomus	+	+	+	+[c]		Lowland evergreen to lower montane
Bunomys coelestis				+		Lower and upper montane
Bunomys andrewsi		+	+			Lowland evergreen
Bunomys heinrichi				+		Lower and upper montane
Bunomys penitus		+	+			Lower and upper montane
Bunomys fratrorum	+					Lowland evergreen to upper montane
Bunomys prolatus		+				Upper montane
Bunomys sp. A		+		+[c]		Lowland evergreen
Bunomys sp. B		+				Lowland evergreen
Paruromys dominator	+	+	+	+[c]		Lowland evergreen to upper montane
Paruromys ursinus				+		Lower and upper montane
Taeromys celebensis	+	+	+	+[c]		Lowland evergreen
Taeromys taerae	+					Lowland evergreen
Taeromys arcuatus			+			Lower montane
Taeromys sp.		+				Lower montane
Taeromys hamatus		+				Lower and upper montane
Taeromys punicans		+		+[c]		Lowland evergreen
Taeromys callitrichus	+	+				Lowland evergreen to upper montane
Taeromys microbullatus			+			Lower montane
Rattus xanthurus	+					Lowland evergreen
Rattus marmosurus	+					Lowland evergreen to upper montane
Rattus facetus		+	+			Lowland evergreen to upper montane
Rattus bontanus				+		Lower and upper montane
Rattus foramineus				+[b]		Lowland evergreen
Rattus pelurus					+	Lowland evergreen
Rattus koopmani					+	Lowland evergreen

TABLE 17—(*Continued*)

Genus and species	Region of Sulawesi: North	Central	Southeast	Southwest	Pulau Peleng	Tropical rainforest formation[a]
Rattus hoffmanni	+	+	+	+[b]		Lowland evergreen to upper montane
Rattus mollicomulus				+		Lower and upper montane

[a] See Whitmore (1984) for definitions and descriptions of these formations.
[b] These records are based on samples from extant populations as well as subfossils.
[c] The occurrences are indicated only by samples of subfossils.

romys celebensis and *Bunomys* sp. were caught about 10 ft away from the other three species on top of thick limbs that are part of the same treefall.

GUNUNG NOKILALAKI (1975)—UPPER MONTANE RAIN FOREST

AMNH 225177 (6800 ft; Mar. 12): On mossy hillside ledge concealed by overhanging tree roots and moss. *Paruromys dominator* was caught on same ledge.

AMNH 225198 (7500 ft; Mar. 24): Trapped on the ground beneath the base of a small tree surrounded by gingers, ferns, rattan rosettes, and short shrubs. *Paruromys dominator* and *Bunomys penitus* were caught in the same place.

AMNH 225199 (7500 ft; Mar. 25): Caught in wet and narrow runway extending beneath and alongside a rotten, wet, and moss-covered tree limb lying on muddy section of a hillside terrace. *Taeromys hamatus, Melasmothrix naso,* and *Tateomys macrocercus* were caught in the same runway.

AMNH 225187 (7400 ft; Mar. 25): Taken on wet ground under pile of wet and rotten sections of trunk, limbs, branches, and other debris tangled about roots of other trees on edge of hillside terrace. *Margaretamys parvus* was caught in the same trap on a different day.

AMNH 225188 (7400 ft; Mar. 26): Caught on damp ground along base of wall-like, hemispheric mat (6 ft high and wide) composed of upturned tree roots, rocks, and soil; covered with dense growth of shrubs, gingers, young pandans, saplings, and moss. *Taeromys hamatus* was trapped in the same spot.

AMNH 225186 (7300 ft; Apr. 4): Caught in runway beneath roots of tall canopy tree on steep, muddy, and rocky side of a ravine; surrounded by undergrowth of small shrubs, gingers, and rattan rosettes. *Maxomys musschenbroekii* was taken in the same place.

AMNH 225202 (7500 ft; Apr. 9): Taken in wide runway beneath rotten, moss-covered tree trunk. *Melasmothrix naso* and *Tateomys macrocercus* were caught in the same spot on the runway.

AMNH 225184 (7200 ft; Apr. 15): Caught on wet runway alongside rotten, moss-covered section of tree trunk lying on muddy and rocky side of ravine. *Eropeplus canus* was caught among boulders just up the hill from the trunk.

AMNH 225192 (7400 ft; Apr. 17): Taken in wet runway beneath rotten, moss-covered tangle of tree trunk and limbs sprawled over very steep and shrubby slope next to rocky ledge. *Tateomys rhinogradoides* was trapped on the ledge.

AMNH 225193 (7400 ft; Apr. 26): In wide runway beneath long, rotten, and moss-covered tree trunk lying on wet hillside in forest. *Bunomys penitus* and *Melasmothrix naso* were caught in the same spot.

The extensive syntopy and sympatry characteristic of *R. hoffmanni* are related to its broad distribution throughout most of Sulawesi (fig. 6) as well as its altitudinal range (table 18), which embraces different tropical evergreen formations at elevations that extend from near sea level to mountain summits. Only five other species of Sulawesian murids have comparable altitudinal distributions (Musser, MSS):

Bunomys fratrorum: Northeastern peninsula
Rattus marmosurus: Northeastern peninsula
Rattus facetus: Central core and southeastern arm
Maxomys musschenbroekii: Central core and all peninsulae
Paruromys dominator: Central core and all peninsulae

Paruromys dominator is the only one of these five species with vertical and horizontal ranges that are concordant with the altitudinal and islandwide distributions of *R. hoffmanni.*

TABLE 18

Altitudinal Distributions of Endemic Murids Occurring in Central Sulawesi[a]

(Numbers indicate elevation in hundreds of meters)

Genus and species	Lowland evergreen rain forest													Montane rain forest										
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Tateomys																									
rhinogradoides																							+	+	+
macrocercus																				+	+	+	+	+	+
Melasmothrix																									
naso																			+	+	+	+	+	+	+
Unnamed genus																									+
Eropeplus																									
canus																			+	+	+	+	+	+	+
Lenomys																									
meyeri						+	+	+	+	+	+	+	+												
Crunomys																									
celebensis									+	+	+	+	+												
Echiothrix																									
leucura	+	+	+	+	+	+	+	+	+	+	+	+	+												
Margaretamys																									
beccarii		+	+	+	+	+	+	+	+	+	+	+	+												
elegans																+	+	+	+	+	+	+	+	+	+
parvus																				+	+	+	+	+	+
Haeromys																									
minahassae		+	+	+	+	+	+	+	+	+	+	+	+												
sp.																		+	+	+	+	+	+	+	+
Bunomys																									
andrewsi	+	+	+	+	+																				
sp. A			+	+	+	+	+	+	+	+	+	+	+												
sp. B										+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
penitus																									
prolatus																				+					
chrysocomus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+						
Taeromys																									
celebensis	+	+	+	+	+	+	+	+	+	+	+	+	+												
punicans	+	+																							
sp.																+	+	+	+	+	+	+	+	+	+
hamatus																									
callitrichus									+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 18—*Continued*

Genus and species	Lowland evergreen rain forest													Montane rain forest										
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Maxomys																									
hellwaldii	+	+	+	+	+	+	+	+	+	+	+														
sp. A											+	+													
sp. B										+	+	+	+	+	+	+	+	+							
dollmani																				+					
wattsi																+	+	+	+	+					
musschenbroekii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Paruromys																									
dominator	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rattus																									
facetus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
hoffmanni	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

[a] The ranges are based primarily on material obtained by Musser during the Archbold Sulawesi Expedition (stored in AMNH and MZB), supplemented with specimens collected by Raven (in UMMZ), Heinrich (in AMNH), and Frost (in BM). The highest record for most species is 2280 m, near the summit of Gunung Nokilalaki. One example of *Tateomys rhinogradoides* and the specimen of the undescribed genus document the 2400-m limit, near the summit of Gunung Tokala (see Musser, 1982b, for map coordinates).

The distribution of *M. musschenbroekii* is slightly more extensive in that this species also occurs on the higher slopes of Gunung Lompobatang where *R. hoffmanni* and *P. dominator* are absent. Horizontal ranges of the others are less expansive, which may be related to the biogeographic history of Sulawesi. *Bunomys fratrorum* and *Rattus marmosurus* are restricted to the northern arm of the island, specifically its eastern and northeastern portions; *Rattus facetus* is found only in the central core and southeastern peninsula (table 17). These two patterns are also common to other members of the Sulawesian mammal fauna, and possibly reflect past episodic isolation in the evolutionary development of flora and fauna during times when Sulawesi was an archipelago instead of the unified entity it is today (Fooden, 1969; Musser, 1987).

In the southwestern arm of Sulawesi, *R. hoffmanni* is found in lowlands, but it is replaced by the morphologically similar *R. mollicomulus* at higher elevations on Gunung Lompobatang, if our interpretation of characters in the few specimens available for study is accurate. In other regions of Sulawesi, however, such replacement of one species by another within the *R. hoffmanni* group does not occur (or if it does, we have not detected it), and this pattern contrasts with the one observed for species in other Sulawesian genera of not only murids, but squirrels and tarsiers as well. In central Sulawesi, for example, there are lowland evergreen forest members that are altitudinally replaced by montane forest counterparts within *Tarsius*; the ground squirrel *Hyosciurus*; and the rats *Margaretamys, Haeromys, Bunomys,* and *Taeromys* (Musser and Dagosto, 1987: 47; table 18). In contrast, *R. hoffmanni* is found throughout all forest formations in that region and its range is sympatric and often syntopic with all of the species in those genera (table 18).

Describing the distribution of *R. hoffmanni* is simple, but uncovering why its altitudinal range presents such an opposite picture to the ones we observe for tarsiers, ground squirrels, and some species of rats is difficult. If the distributional pattern of *R. hoffmanni* is the result of dispersal rather than vicariant events, its presence in most regions of Sulawesi, and especially in the central core, may represent a more recent dispersal into those areas as compared to the other species. Other explanations, however, may better fit the distributional data, and these will be explored later in a context analyzing horizontal and altitudinal distributional patterns of all the endemic Sulawesian mammals (Musser, in prep.).

Future Inquiry

To which other species of *Rattus* are members of the *R. hoffmanni* group most closely related? Where does *R. koopmani* fit within the framework of phylogenetic relationships among species of the genus? These questions define the direction of future studies. When we began our analyses for this report, we thought it would be possible to determine if *R. koopmani* was a member of the *R. hoffmanni* group, but we could not. Diagnostic morphological features of the holotype, the only specimen of *R. koopmani* that we have seen, do not fit neatly within the character boundaries defining *R. hoffmanni* and *R. mollicomulus.* For example, in proportions of certain external and cranial dimensions, *R. koopmani* resembles *R. elaphinus* of Pulau Taliabu and not *R. hoffmanni* of Sulawesi (fig. 34), yet in some qualitative traits associated with the skull and dentition, the holotype of *R. koopmani* bears close resemblance to examples of *R. hoffmanni.* We simply need to study more specimens of *R. koopmani* before we can make reasonably definitive statements about its possible relationships. By contrast, *R. hoffmanni* is represented by hundreds of specimens and comparisons of the morphology of these with samples of other *Rattus* species native to the Indo-Australian region may reveal the closest relatives of *R. hoffmanni* and *R. mollicomulus,* and possibly the geographic region of their ancestral origins.

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Pseudoryzomys simplex (Rodentia: Muridae) and the Significance of Lund's Collections from the Caves of Lagoa Santa, Brazil

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ABSTRACT

Collections of Quaternary mammals excavated from caves near Lagoa Santa, Brazil, by Peter Wilhelm Lund in the first half of the 19th century include a diverse extinct megafauna together with many extant species of marsupials, bats, edentates, lagomorphs, rodents, carnivores, and ungulates. Muroid rodents are represented by 25 species in the cave faunas, but the unresolved systematics of these animals prohibit unambiguous taxonomic identifications without careful comparisons of the type material in Copenhagen with other specimens. Our reexamination of the syntypes of *Hesperomys simplex,* described by Herluf Winge in 1887 from skeletal material found in the Lagoa Santa caves, reveals that this muroid species is the same as *Pseudoryzomys wavrini,* an uncommon rat named by Oldfield Thomas in 1921 from Recent specimens. We redescribe *Pseudoryzomys simplex* and summarize what little is known of its ecological and geographical distribution. Future systematic studies of other Lagoa Santa muroids will facilitate stronger historical and biogeographical inference from Lund's important collections despite irresolvable problems of stratigraphic control.

RESUMO

As coleções de mamíferos quaternários escavadas por Peter Wilhelm Lund em cavernas próximas a Lagoa Santa, Brasil, durante a primeira metade do século XIX contêm uma variada megafauna extinta associada a várias espécies viventes de marsupiais, morcegos, desdentados, lagomorfos, roedores, carnívoros, e ungulados. Roedores muróideos estão representados por 25 espécies nas faunas cavernícolas, porém a precária sistemática destes animais impede identificações taxonômicas precisas sem a realização de comparações cuidadosas entre o material tipo de Copenhagen e outros espécimens. Nosso reexame dos síntipos de *Hesperomys simplex,* descrito por Herluf Winge em 1887 com base em material esquelético encontrado nas cavernas de Lagoa Santa, revela que esta espécie muróide é idêntica a *Pseudoryzomys wavrini,* um rato pouco comum descrito por Oldfield Thomas em 1921 com base em espécimens recentes. Neste trabalho redescrevemos *Pseudoryzomys simplex* e resumimos o pouco que se sabe sobre a sua ecologia e distribuição geográfica. Futuros estudos sistemáticos de outros muróideos de Lagoa Santa facilitarão a realização de melhores inferências históricas e biogeográficas baseadas nas importantes coleções de Lund, apesar dos irresolvíveis problemas de controle estratigráfico.

RESUMEN

Las colecciones de mamíferos cuaternarios excavadas en las cuevas cercanas a Lagoa Santa, Brasil, por Peter Wilhelm Lund en la primera mitad del siglo XIX incluyen una megafauna diversa y extincta, junto con otras muchas especies vivientes de marsupiales, murciélagos, edentados, lagomorfos, roedores, carnívoros, y ungulados. Los roedores muroides están representados en las faunas

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de las cuevas por 25 especies, pero la sistemática no resuelta de estos animales no permite identificaciones taxonómicas inequívocas sin comparar el material típico en Dinamarca con otros especímenes. Nuestra reexaminación de los sintipos de *Hesperomys simplex,* descritos por Herluf Winge en 1887 con material óseo de las cuevas de Lagoa Santa, revelan que este especie muroide es la misma que *Pseudoryzomys wavrini,* una rata nombrada por Oldfield Thomas en 1921 de especímenes recientes. Redescribimos *Pseudoryzomys simplex* y resumimos lo poco que se conoce de su ecología y distribución geográfica. Futuros estudios sistemáticos de otros muroides de Lagoa Santa deberán facilitar inferencias históricas y biogeográficas más confiables de estas colecciones importantes de Lund, a pesar de problemas no resolubles de control estratigráfico.

INTRODUCTION

The Danish naturalist Peter Wilhelm Lund left Copenhagen on 12 November 1832 bound for Brazil, from which distant land he never returned. A young but respected colleague of Cuvier, Milne-Edwards, and von Humboldt, and a relative of Søren Kierkegaard, Lund was deeply involved with the contemporary intellectual life of continental Europe; nevertheless, he was to spend all his remaining years at Lagoa Santa, a remote village in the Brazilian state of Minas Gerais. There, from limestone caves along the valley of the Rio das Velhas, Lund excavated, described, and shipped to Denmark, between 1835 and 1849, one of the largest collections of fossil mammals yet known from South America (Paula Couto, 1950; Simpson, 1984).

Although Lund reported his discoveries in an important series of memoirs that were sent as manuscripts from Brazil and published by the Royal Danish Scientific Society, the herculean task of properly monographing his enormous collections fell to another Dane whom he never met, Herluf Winge. Winge's multivolume treatise (written with only a few collaborators), entitled *E Museo Lundii* and published between 1887 and 1915, described 151 species of mammals (including humans) from the cave deposits. In addition, Winge described living species of mammals that had been collected in the neighborhood of Lagoa Santa by Lund and his colleagues.

Lund's collections provide an important record of the extinct mammalian megafauna of the Brazilian Quaternary: ground sloths, glyptodonts, litopterns, notoungulates, horses, camels, gomphotheres, bears, and saber-toothed cats. Truly remarkable, however, is the diversity of small mammals represented: large numbers of marsupials, bats, and rodents collected by Lund were meticulously described and illustrated by Winge. Muroid rodents, a group that is seldom adequately sampled in fossil or Recent faunal inventories, were among the first subjects of Winge's systematic studies (Winge, 1887); 25 species were reported from the cave deposits, far more than are known from any other South American paleofauna. Many, but not all, of the muroid species reported as fossils were also represented among the specimens collected as living animals in the forests and savannas around Lagoa Santa. Some muroids, although not collected alive, were judged by Winge to have survived to Recent times on the basis of their presence in fresh owl pellets.

That an extinct megafauna should be found associated with the remains of many extant species of small mammals is far from unprecedented in the literature of Quaternary paleontology (Martin, 1984), but a well-documented example of size-dependent extinctions based on materials as abundant as those of the Lund collections would be an important contribution to Neotropical historical biogeography. Considerable fossil evidence reveals that present-day faunas of large South American mammals are only relicts of more diverse communities that existed in the not-too-distant past (Marshall et al., 1984), but the possibility that Recent South American faunas of smaller mammals represent essentially intact continental radiations (Voss, 1988) remains unevaluated for lack of evidence. Unfortunately, the prospect for historical biogeographic analyses of the Lagoa Santa fossils from their literature has been clouded by questions of stratigraphic control, by linguistic difficulties (Winge wrote only in Danish), and by the unresolved systematics of many groups of small South American mammals.

Our interest in Lund's collections was prompted by Massoia's (1980) suggestion that *Hesperomys simplex,* a muroid rodent named by Winge in 1887 from skeletal material obtained in the Lagoa Santa caves, is a member of the extant genus *Pseudoryzomys. Pseudoryzomys* had previously been thought to contain only *P. wavrini,* an obscure rat first described as a species of *Oryzomys* by Thomas (1921), based on two skins with skulls collected by the Marquis de Wavrin in the Chaco Boreal of Paraguay. Hershkovitz (1962) redescribed aspects of the external, cranial, and dental morphology of *wavrini* and erected the genus *Pseudoryzomys* to contain it. Neither Thomas (1921) nor Hershkovitz (1962) compared *wavrini* with *simplex.* Massoia (1980) is nevertheless correct; in fact, *Hesperomys simplex* and *Pseudoryzomys wavrini* are names that apply to the same species, a conclusion supported by comparisons provided in this paper. We redescribe *Pseudoryzomys simplex* based on our examination of Winge's type series and recently collected material, document the geographic range of the species based on specimens in museum collections, and summarize what little can be inferred about the ecology of *P. simplex* from trapping records and collectors' field notes.

The problem of *Pseudoryzomys simplex* provides a concrete example of the taxonomic difficulties that will be encountered in future efforts to interpret the historical and biogeographic significance of Lund's collections from the caves of Lagoa Santa. Because those collections offer a rare opportunity to evaluate important hypotheses concerning the evolutionary history of South American mammals, however, we emphasize that such difficulties can be surmounted with appropriate systematic research efforts.

Materials and Methods

Specimens: The specimens upon which this report is based are deposited in the collections of the American Museum of Natural History, New York (AMNH); the British Museum of Natural History, London (BMNH); the University of Connecticut Museum of Natural History, Storrs (CONN); the Field Museum of Natural History, Chicago (FMNH); the University of Michigan Museum of Zoology, Ann Arbor (UMMZ); the National Museum of Natural History, Washington, D.C. (USNM); and the paleontological collections of the Universitets Zoologisk Museum, Copenhagen.

Measurements, Anatomy, and Cytology: External dimensions (total length, TL; length of tail, LT; length of hind foot, HF; and length of ear from notch, Ear) were measured according to the standard American protocol described by Hall and Kelson (1959: 1040–1041) or are presumed to have been so measured (except by British and European collectors). Head-and-body length (HBL) was obtained by subtracting LT from TL. We measured the undistorted dried hind feet of museum skins and report this dimension rather than the collector's original measurement except where noted.

Cranial dimensions were measured with dial calipers and recorded to the nearest 0.05 mm. Condylo-incisive length (CIL), length of diastema (LD), length of molars (LM), breadth of M1 (BM1), length of the incisive foramina (LIF), breadth of the palatal bridge (BPB), breadth of the zygomatic plate (BZP), least interorbital breadth (LIB), breadth of braincase (BB), and depth of the incisor (DI) were measured as described and illustrated by Voss (1988). Breadth of the rostrum (BR) is the transverse dimension across the maxillae, measured inside the notches formed where the anteroventral margin of the zygomatic plate joins the rostrum on each side. Length of the orbital fossa (LOF) is the greatest inside dimension of the orbit, measured between the maxillary and squamosal roots of the zygomatic arch.

Characters of the viscera and male genitalia were determined by dissection of fluid-preserved specimens fixed in 10% formalin and stored in 70% alcohol. Anatomical terminology employed herein follows usages established or referenced by Reig (1977), Carleton (1980), and Voss (1988).

Somatic metaphase chromosome preparations were obtained from bone marrow cells using minor modifications of Patton's (1967) standard in vivo colchicine/hypotonic citrate protocol.

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Erika Bach analyzed the chromosome preparations of AMNH 262048. The epoxy casts of molars illustrated in figure 2 were prepared by Jane Shumsky, and the SEM images were taken by Peling Fong. Photographs of skeletal material, specimen labels, and bibliographic materials are the work of Peter Goldberg. Pat Brunauer and Muriel Williams word-processed the manuscript with their usual tolerance of repeated revisions. We thank Michael Carleton, Ross MacPhee, and Guy Musser for reading the penultimate draft and offering helpful suggestions for its improvement.

We take great pleasure in dedicating this paper to Karl Koopman, whose commitment to systematic mammalogy has been an inspiration to us both.

THE TAXONOMIC BACKGROUND

Winge (1887) named *Hesperomys simplex* from skeletal material found near Lagoa Santa in owl pellets of Recent origin ("*Uglegylp fra nyeste Tid*") and in cave sediments ("*Hulernes Jordlag*"). Lund used Portuguese names for the caverns (*lapas*) that he excavated, and referred to chambers within them by number. Winge reported specimens of *Hesperomys simplex* from *Lapa da Escrivania Nr. 5, Lapa da Escrivania Nr. 11, Lapa da Lagoa do Semidouro, Lapa do Marinho Nr. 2,* and *Lapa da Serra das Abelhas.* We have not been able to locate any map of the valley of the Rio das Velhas near Lagoa Santa on which these caves are shown.

Winge compared *Hesperomys simplex* with three other congeners from Lagoa Santa: *H. tener* and *H. expulsus,* small mice known both from cave material and living specimens; and *H. molitor,* a large rat known only from skeletal fragments found in caves. Winge's comparisons are lengthy and need not be repeated here because they belabor the obvious fact that *H. simplex* is entirely unlike any other muroid in the Lagoa Santa faunas, ancient or extant.

Winge employed the genus *Hesperomys* to contain "generalized" New World muroids whose molars have low, tubercular cusps and lack well-developed mesolophs and mesolophids (see Winge, 1941: 41–43, for the sense in which *Hesperomys* and other Lagoa Santa muroid genera are to be understood). Species with well-developed mesolophs and mesolophids were placed by Winge in the genus *Calomys.* Both *Hesperomys* and *Calomys,* however, have the same type species, *Mus bimaculatus* Waterhouse, 1837, and *Hesperomys* is now regarded as a strict junior synonym of *Calomys* (see Hershkovitz, 1962: 129–130, for the tortuous history of these names). All of the species that Winge referred to *Hesperomys* and *Calomys* were transferred to *Oryzomys* by Trouessart (1898), but *tener* and *expulsus* have subsequently been assigned to *Calomys. Oryzomys molitor* was ignored in the systematic literature after Trouessart until Massoia (1980) suggested that it belongs in the genus *Holochilus.*

Ellerman (1941) regarded *simplex* as *Oryzomys* incertae sedis, but Cabrera (1961) placed *simplex* in the nominate subgenus of *Oryzomys,* remarking that "*La posición de esta especie es por el momento un poco dudosa*" (surely an understatement, because there is no evidence that anyone after Winge ever bothered to examine the specimens in Copenhagen). Unbeknownst to (or at least uncited by) Cabrera, Moojen (1952) had earlier referred *simplex* to the genus *Oecomys,* but Hershkovitz (1960) rejected that assignment on the basis of characters described and figured by Winge. Hershkovitz (1962) later listed *simplex* as a "Pleistocene" form of *Calomys* despite Winge's statement that some of the Lagoa Santa material was of Recent origin.

Meanwhile, Thomas (1921: 178) had described *Oryzomys wavrini* from Paraguay as a "very distinct swamp-rat . . . readily distinguishable by its intermediate size, its comparatively short tail, most *Oryzomys* having this organ longer than the head and body, its unridged supraorbital edges, concave zygomatic plate, and the obsolescence of the cross-crochets [mesolophs and mesolophids] in the molars. Important as the last character usually is, the animal is so essentially an *Oryzomys* in all other respects that I do not think there is any doubt that its proper place is in that genus. Possibly even the reduction of the crochets is a mere abnormality."

The species *wavrini* was removed from *Oryzomys* by Hershkovitz (1959), who proposed a new genus, *Pseudoryzomys,* to contain it. He remarked (1959: 8–9) that "The type and only species of the genus resembles *Oryzomys palustris* [the type species of *Oryzomys*] in size, external appearance, and, very probably, in habits. Cranial and dental characters of *wavrini,* however, prove it to be more nearly related to *Phyllotis* than to any oryzomyine." As Pine and Wetzel (1975) observed, the above statement (which is the only description of *Pseudoryzomys* offered by Hershkovitz in 1959) is insufficient to make the name available under the International Code of Zoological Nomenclature, so *Pseudoryzomys* as a valid genus-group taxon dates from 1962, when Hershkovitz first provided an explicit account of characters distinguishing it from other Neotropical muroids.

The separate threads of these two taxonomic histories converged when Massoia (1980) suggested that *simplex* and *wavrini* are congeners, basing his judgment on Winge's (1887) illustration of a partial skull and mandible of the former. Our examination of the type material of *simplex* and of all the specimens of *wavrini* in North American and European museums convinces us that the two taxa are not only congeneric but conspecific: *wavrini* is a subjective junior synonym of *simplex,* and *Pseudoryzomys* is the appropriate genus to contain them. We rediagnose and redescribe *Pseudoryzomys simplex* below; because *Pseudoryzomys* is monotypic, the diagnosis and description apply to both genus and species.

Pseudoryzomys simplex (Winge, 1887)

Hesperomys simplex Winge, 1887: 11.
Oryzomys simplex Trouessart, 1898: 528.
Oryzomys wavrini Thomas, 1921: 177.
Oecomys simplex Moojen, 1952: 55.
Pseudoryzomys wavrini Hershkovitz, 1959: 8; and Hershkovitz, 1962: 208, in which *Pseudoryzomys* was first made formally available.
Calomyx simplex Hershkovitz, 1962: 123.
Pseudoryzomys wavrini reigi Pine and Wetzel, 1975: 649.
Pseudoryzomys simplex Massoia, 1980: 282.

LECTOTYPE[3]: An uncataloged partial cranium from *Lapa da Escrivania Nr. 5,* near Lagoa Santa in Minas Gerais, Brazil. The specimen (fig. 1) consists of the rostrum, palate, zygoma, and anterior braincase of an adult animal with a completely erupted and moderately worn molar dentition (fig. 2A). The type lacks both nasal bones, the right first and third molars, parietals, interparietal, auditory bullae, and the entire occiput. The specimen can be identified as the one illustrated in plate II of Winge (1887) by a paper label bearing the Danish word "*Tegnet*" ("drawn") in Winge's handwriting. Because the 1887 illustration (reproduced in fig. 1) shows both nasals and a complete molar dentition in place, the bones and teeth presently missing from the type may have been lost sometime in the subsequent century. Alternatively, the 1887 illustration may have been a partial reconstruction based on other specimens as well. Included in the same labeled box with this partial cranium is a single right mandible; since, however, the molars of the upper dentition are well worn (fig. 2A) while the mandibular dentition is unworn (fig. 2C), we doubt that the two elements are from the same individual and we restrict the lectotype to the partial cranium alone.

PARALECTOTYPES: In addition to the lectotype there are 24 skull fragments bearing

[3] Winge did not designate either a holotype or a type series; therefore, all of the specimens he examined must be considered syntypes. We presume these to consist of the material labeled, on small rectangles of brittle, grayish paper, in the same cursive script as that which appears on the plates of the 1887 monograph. Of the syntypes thus identified, we select the most complete specimen as lectotype, by which action the remainder become paralectotypes (CODE, 1985).

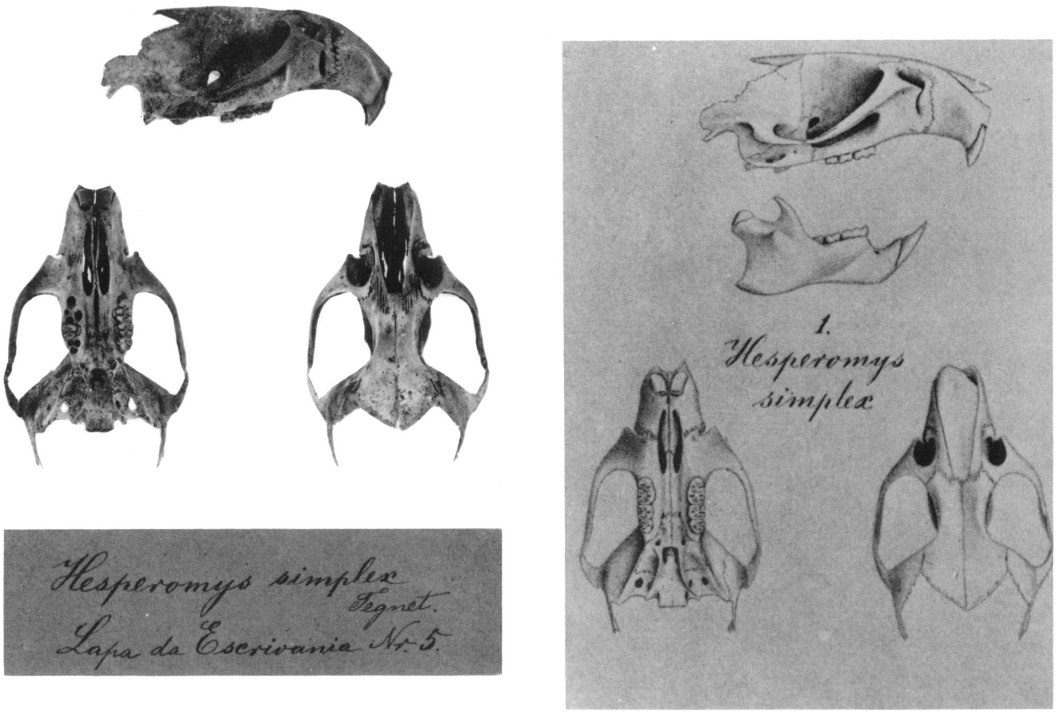

Fig. 1. The lectotype of *Pseudoryzomys simplex* with its label **(left)**, and Winge's (1887) illustration **(right)**.

partial or complete upper molar series that can be positively identified as *Pseudoryzomys simplex*; of these, 12 are from *Lapa da Escrivania Nr. 5* and 12 are labeled "*Uglegylp fra nyere Tid*" ("owl pellets of more recent times"). Mandibles of *Pseudoryzomys simplex* are much more numerous in the collection and are labeled from *Lapa da Escrivania Nr. 5, Lapa da Escrivania Nr. 11,* and *Lapa da Lagoa do Semidouro.* Winge (1887) also reported *P. simplex* from *Lapa do Marinho Nr. 2* and *Lapa da Serra das Abelhas,* but we found no specimens from these localities in the collections.

REMARKS: Although fragmentary, there is enough material from the Lagoa Santa caves for comparisons with recently collected specimens (hitherto identified as *wavrini*) in many qualitative and a few quantitative characters. No qualitative differences are apparent in the morphology of the rostrum, zygomatic notches, zygomatic arches, zygomatic plates, interorbital region, incisive foramina, bony palate, mesopterygoid fossa, parapterygoid fossae, carotid arterial supply, mandibles, incisors, molar occlusal surfaces, and molar roots. Cranial and dental measurements of the Lagoa Santa specimens overlap broadly with those of Paraguayan and Bolivian examples (tables 1, 2). There is, therefore, no observational basis for distinguishing *simplex* and *wavrini,* which are henceforward regarded as synonyms. On this assumption, the diagnosis and description provided below ascribe to *P. simplex* many characters that can only be determined from anatomically complete, Recent materials.

DIAGNOSIS: Rodents belonging to the murid subfamily Sigmodontinae (sensu Carleton and Musser, 1984) with grizzled-brownish dorsal pelage; tail bicolored and about as long as head-and-body; hind feet narrow with small webs present among digits II, III, and IV; mammae eight (pectoral pair of teats present); interorbital region constricted, with sharp-edged or beaded, convergent posterior margins; incisive foramina long and parallel-sided; bony palate long with prominent pos-

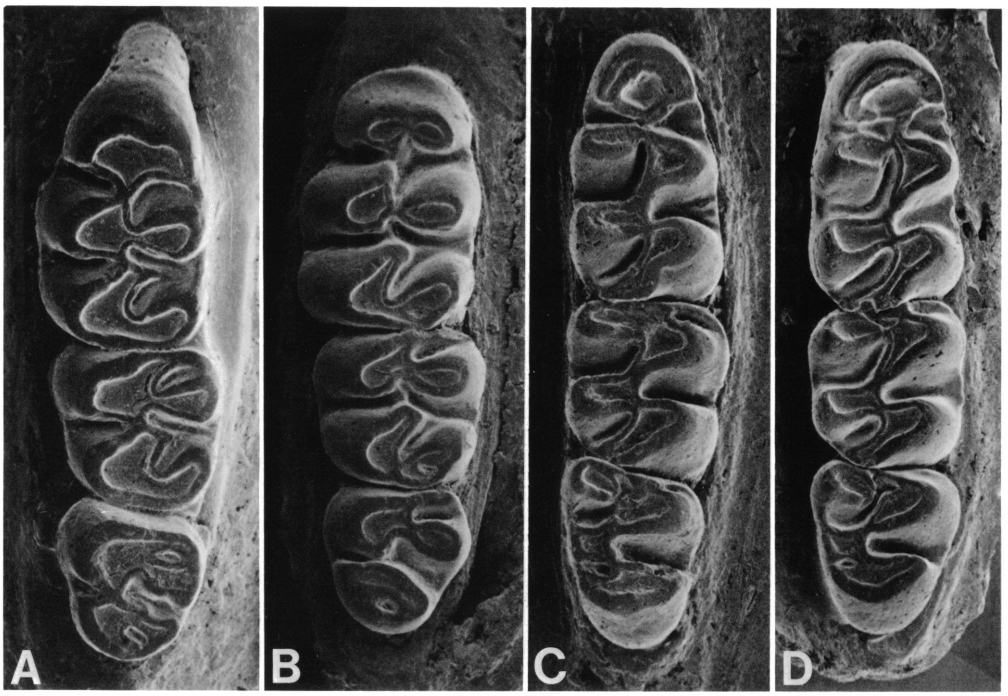

Fig. 2. Left maxillary (**A, B**) and right mandibular (**C, D**) molars of *Pseudoryzomys simplex*. **A.** The lectotype. **B, D.** A Paraguayan specimen (CONN 17060). **C.** A paralectotype.

terolateral pits; large sphenopalatine vacuities present; parapterygoid fossae narrow; carotid circulation highly derived; upper incisors ungrooved and opisthodont; anterocone/id of M1/m1 undivided; upper molars with labial and lingual cusps arranged in opposite pairs; small mesolophs on M1 and M2 project from median mures but do not reach labial cingulum; lower molars with alternating labial and lingual cusps, without mesolophids; M1 and m1 each with four roots; stomach unilocular and hemiglandular; glans penis complex, with tridigitate baculum.

MORPHOLOGICAL DESCRIPTION: Body pelage long and soft; grizzled-brownish or -grayish dorsally, straw-colored or buffy below, but the bases of ventral hairs always dark gray. Mystacial, superciliary, genal, submental, interramal, and carpal vibrissae present; mystacial vibrissae not very long, not extending beyond pinnae when laid back against cheek. Pinnae small, covered with short hairs colored like fur of head, not appearing naked. Manus and pes covered dorsally with short, pale hairs; distinctly longer hairs on last phalanges of pes seldom extend beyond tips of claws. Plantar surface of manus with two carpal and three interdigital pads; densely set with small epidermal tubercles. Hind feet long and narrow, with digits II–IV much longer than I and V (claw of I extends less than half the length of first phalange of II; claw of V extends almost to first interphalangeal joint of IV). Plantar surface of hind foot densely set with small epidermal tubercles distally (heel is smooth); with one or two small metatarsal pads (the lateral, hypothenar pad may be present[4] or absent) and four very small interdigital pads; small webs of skin, present between digits II, III, and IV, seldom extend more than about half the length of the first phalanges. Tail about as long as head-and-body; covered with short hairs, but underlying epidermal scales clearly visible; without

[4] Hershkovitz (1962) and Olds and Anderson (1989) reported that *Pseudoryzomys* has only five plantar pads rather than the six commonly observed among other Neotropical muroids. The missing tubercle is the hypothenar (lateral metatarsal pad), but in at least one specimen (UMMZ 133912) a distinct hypothenar pad is present along with the thenar and four interdigital pads.

TABLE 1

Sex and Measurements (in millimeters) of Adult *Pseudoryzomys simplex* from Lagoa Santa (Brazil) and from Paraguay

(Sample mean, range [in parentheses], and sample size are provided in each column)

	Lagoa Santa		
	Lapa da Escrivania[a]	Recent owl pellets[b]	Paraguay[c]
Sex			5 males, 5 females, 1 unk.
HBL			**115** (103–127) 9
LT			**116** (102–133) 10
HF			**28** (27–31) 7
Ear			**16** (13–19) 8
CIL			**26.05** (24.65–27.45) 11
LD	**8.20** (7.80–8.90) 6	**8.50** (8.50) 1	**7.25** (6.65–7.65) 10
LM	**4.95** (4.65–5.40) 9	**4.95** (4.60–5.25) 9	**4.70** (4.55–4.85) 10
BM1	**1.55** (1.50–1.65) 11	**1.55** (1.45–1.70) 11	**1.50** (1.45–1.60) 11
LIF	**6.65** (5.90–7.20) 6	**6.60** (6.60) 1	**5.95** (5.70–6.30) 11
BR	**5.00** (4.65–5.15) 4	**5.45** (5.45) 1	**4.35** (3.90–4.75) 11
BPB	**3.10** (2.80–3.25) 4		**2.40** (2.10–2.65) 9
BZP	**3.25** (2.50–3.80) 12	**3.15** (2.70–3.80) 7	**2.95** (2.65–3.20) 11
LIB	**4.00** (3.90–4.15) 5		**3.75** (3.45–3.90) 11
BB	**12.20** (12.20) 1		**12.00** (11.50–13.00) 11
DI	**1.75** (1.75) 1	**1.75** (1.75) 1	**1.45** (1.30–1.60) 11
LOF	**11.25** (11.25) 1		**10.45** (10.10–11.05) 11

[a] The lectotype and 12 paralectotypes of *P. simplex,* uncataloged.

[b] Twelve paralectotypes of *P. simplex,* uncataloged.

[c] BMNH 20.12.18.15, 20.12.18.16 (type of *P. wavrini*); CONN 15678, 15741, 15757, 15910, 16487, 16488, 17060; UMMZ 133912, 133913.

TABLE 2

Sex and Measurements (in millimeters) of Adult *Pseudoryzomys* from Bolivia

	Departamento Beni				Santa Cruz:	
	AMNH 210054	AMNH 262048	FMNH 118810	USNM 364749	USNM 390668	Mean
Sex	male	female	male	female	female	
HBL	123	117	140	110	94	**117**
LT	130	132	140	105	132	**128**
HF	33	30	33	29	28[a]	**31**
Ear	18	18	17	15	18	**17**
CIL	29.50	28.35	28.90	—	28.00	**28.70**
LD	8.40	8.25	8.60	7.00	7.90	**8.00**
LM	5.00	4.70	4.85	5.00	4.75	**4.85**
BM1	1.55	1.50	1.45	1.55	1.55	**1.50**
LIF	6.55	6.40	6.45	5.75	6.40	**6.30**
BR	4.90	4.60	5.20	4.20	4.70	**4.70**
BPB	2.60	2.90	2.80	2.20	3.10	**2.70**
BZP	3.70	3.25	3.30	2.90	3.25	**3.30**
LIB	4.40	4.10	4.05	4.10	4.25	**4.20**
BB	12.65	12.35	—	12.15	12.50	**12.40**
DI	1.90	1.65	1.70	1.40	1.70	**1.65**
LOF	11.00	11.00	—	10.05	11.20	**10.80**

[a] Collector's measurement.

terminal pencil or tuft of distinctly longer hairs; bicolored (dark above, pale below). Eight mammae in inguinal, abdominal, postaxial, and pectoral pairs.

Skull (fig. 3) with conspicuously short rostrum, deep zygomatic notches, and narrow interorbital region in dorsal view; posterior supraorbital margins convergent and sharp-edged, sometimes beaded; zygomatic arches widest across squamosal roots, convergent anteriorly. Braincase not conspicuously inflated, without prominent temporal ridges or large lambdoidal crests. Zygomatic plate (inferior zygomatic root) broad, with straight or concave anterior margin, and often with small, blunt anterodorsal process. Incisive foramina narrow and parallel-sided (slightly wider behind the premaxillary-maxillary suture) and long, usually extending posteriorly to or between anterocones of first molars. Palate smooth, without deep furrows or median ridges; sometimes with small median posterior process; long, extending posteriorly well behind third molars; with prominent posterolateral palatal pits. Bony roof of mesopterygoid fossa perforated by large sphenopalatine vacuities. Parapterygoid fossae not deeply excavated; narrow, without greatly expanded lateral margins. Buccinator-masticatory foramen and accessory oval foramen separted by bony strut of alisphenoid, or confluent (alisphenoid strut absent). Stapedial foramen absent or minute; ophthalmic and maxillary circulation supplied by branch of internal carotid artery arising internally on floor of braincase. Auditory bullae small and flask-shaped. Large postglenoid foramen and smaller subsquamosal fenestra perforate lateral wall of braincase above bulla. Mandible short and deep with large, falciform coronoid process; tip of angular process below or slightly behind articular condyle; capsular process of lower incisor alveolus below or just posterior to base of coronoid process.

Upper incisors smooth (not grooved), narrow, and opisthodont with yellow-orange enamel bands. Upper molar rows parallel; molars (fig. 2) low-crowned and bunodont even when unworn. Principal labial and lingual cusps strictly opposite in upper teeth, directly connected across midline of tooth by transverse lophs. First upper molar with broad, undivided anterocone (separate labial and lingual conules, present on some newly erupted teeth, disappear quickly with wear); discrete anteroloph absent on first upper molar, well developed on second and third; small mesoloph projecting from median mure but not contacting mesostyle on first and second upper teeth; small posteroloph present on unworn M1–M3. First upper molar with four roots, the fourth (labial) root conspicuous above paracone in old adult specimens; second and third upper molars with three roots (anterior, posterior, and lingual) each. Lower molars with principal labial and lingual cusps alternating in anteroposterior position. Anteroconid of first lower molar undivided; anterolophids and mesolophids absent from all lower teeth; large posterolophids present on first and second lower molars, occasionally absent from third. First lower molar with four roots: one anterior, one posterior, one lingual (below metaconid), and one labial (below protoconid); second and third molars with three roots each (two anterior and one posterior).

Fig. 3. Skull and mandible of a Paraguayan specimen of *Pseudoryzomys simplex* (CONN 16488).

First rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; second thoracic vertebra with greatly elongated neural spine; thoracicolumbar vertebrae 19 or 20; sacrals 3 or 4; caudals about 29 (counts from four specimens). Humerus without entepicondylar foramen. Stomach unilocular and hemiglandular. Gall bladder apparently absent (observation from one specimen dissected for tissues in field). One pair of preputial glands present (other male accessory reproductive glands undetermined). Glans penis spinous externally; complex, with deep terminal crater containing three bacular mounds supported by tridigitate baculum, and a bifurcate urethral flap.

KARYOTYPE: Analyzable preparations of somatic metaphase chromosomes are available from two specimens, both females, from Paraguay (UMMZ 133913) and Bolivia (AMNH 262048). The two preparations yield identical karyotypes with diploid numbers of 56 and fundamental numbers (excluding the indistinguishable sex chromosomes) of 54. The chromosomes grade evenly from large to small, and all centromeres appear to be terminally located. One poor preparation from a male Paraguayan specimen (UMMZ 133912) is impossible to analyze with confidence, but no obviously biarmed elements are visible and the total count is about 56.

COMPARISONS: Although it is not an object of this report to analyze hypotheses of phylogenetic relationships, we observe that *Pseudoryzomys simplex* is conspicuously more similar to some oryzomyines than to members of the phyllotine group in which it was classified by Hershkovitz (1962). Anatomical resemblances with *Oryzomys palustris* and certain other species in the nominate subgenus of *Oryzomys* are especially striking, and include aspects of the morphology of the hind foot, number of mammae, palatal morphology, auditory bullar form, carotid arterial supply, molar occlusal morphology and root number, number of preputial glands, absence of the gall bladder, and stomach morphology (see Carleton, 1980, and Carleton and Musser, 1989, for descriptions and illustrations of character states in *O. palustris*). Were it not for the diminutive mesolophs in the upper dentition and the absence of mesolophids in the lower, there would appear to be no characters that distinguish *Pseudoryzomys* from the oryzomine group as diagnosed by Hershkovitz (1944, 1960).

Concordant patterns of similarity are evident from chromosomal comparisons. The karyotype of *P. simplex* is grossly indistinguishable from that of the oryzomyine *Sigmodontomys alfari,* and closely resembles those of *Oryzomys palustris* (2N = 56, FN = 56) and *O. xantheolus* (2N = 56, FN = 58) as illustrated and described by Gardner and Patton (1976). By contrast, a substantial number of Robertsonian and non-Robertsonian rearrangements would be necessary to transform any of the phyllotine karyotypes reported by Pearson and Patton (1976) to that reported here for *P. simplex.*

Although we concur, in effect, with the recent decision of Olds and Anderson (1989) to remove *Pseudoryzomys* from the tribe Phyllotini, we decline to perpetuate the traditional phenetic practices of Neotropical muroid classification by recommending that the genus instead be assigned to the Oryzomyini. In the absence of substantive phylogenetic analyses of character data, it cannot be determined whether the Oryzomyini as currently constituted (by Reig, 1980, 1984) is monophyletic, paraphyletic, or just a heterogeneous collection of genera united by their common possession of well-developed mesolophs and meslophids. Referring *Pseudoryzomys* to the Oryzomyini would effectively render the tribe undiagnosable with no compensating heuristic advantage in terms of implied relationships. Until such time as compelling cladistic evidence is available to classify *Pseudoryzomys* in a phylogenetically meaningful group, it is best left in its current ambiguous position as Sigmodontinae incertae sedis.

DISTRIBUTION: Specimens that we have examined document the occurrence of *Pseudoryzomys simplex* in extreme eastern Brazil (Estado Pernambuco), central Brazil (Minas Gerais), western Paraguay (Departamento Presidente Hayes), eastern Bolivia (Departamentos Beni and Santa Cruz), and northern Argentina (Provincia Formosa). Massoia (1980) stated that *Pseudoryzomys* also occurs in Departamento Chaco, Argentina. So few specimens are available, however, that the known range of the species may be expected

to expand significantly with future collecting efforts.

GEOGRAPHIC VARIATION: Measurements of Brazilian, Paraguayan, and Bolivian specimens (tables 1, 2) suggest that populations of *Pseudoryzomys simplex* from the Chaco average smaller in most anatomical dimensions than populations to the east and west. Pine and Wetzel (1975) proposed the subspecific epithet *P. wavrini reigi* for the larger Bolivian animals to distinguish them from smaller Paraguayan specimens that they allocated to *P. w. wavrini.* Brazilian specimens, however, including Recent material from Pernambuco (whose measurements are not tabulated here) and the Lagoa Santa cave collections, average as large or larger than the Bolivian sample. Bolivian skins appear somewhat darker than Paraguayan skins, but too few specimens are available to evaluate subtle differences in pelage color among our series. We have not examined any skins of Brazilian specimens.

Although the Paraguayan sample averages smaller than Brazilian and Bolivian series, we note that the available karyotypes from Paraguay and Bolivia are identical and that no qualitative external, cranial, or dental traits provide evidence of conspicuous population differentiation. Many species of bats are smaller and paler in the Chaco than in surrounding areas (Myers and Wetzel, 1983), and it may be that *Pseudoryzomys simplex* conforms to that ecogeographic pattern. If a trinomial classification were to be judged useful in future revisionary studies based on larger and better distributed samples than are presently available, the names *simplex, wavrini,* and *reigi* are all valid and available for that purpose. At present, however, we see no point in retaining a subspecific nomenclature.

ECOLOGY: Most Recent collections of *Pseudoryzomys simplex* are from the Chaco Boreal of western Paraguay, northern Argentina, and southeastern Bolivia. This is a flat, monotonous landscape, mostly below 500 m elevation, through which sluggish, sediment-laden streams meander southeastward to the Río Paraguay. Marshes and palm savannas, often dissected by dense gallery forests, predominate in the eastern Chaco, but thornscrub and grasslands are typical of the more xerophytic western vegetation. Rainfall is seasonal and varies from year to year in timing and amount. Chaco soils are typically formed of impermeable clays overlying saline sands; drainage is poor and extensive flooding usually follows heavy rains (see Myers and Wetzel, 1983, for references concerning chacoan vegetation, geology, and climate).

Three specimens of *Pseudoryzomys simplex* were collected near Villa Hayes in the eastern Chaco of Paraguay. All were trapped on the ground under dense grass in "*pantanal,*" an open savanna habitat dominated by the palm *Copernica australis* (fig. 4). These animals were taken within a few hundred meters of standing water, but the entire savanna is probably inundated to a depth of at least a few inches in wet weather. Adjacent patches of woodland, growing on slightly elevated soils, are characterized by thorny legumes (chiefly *Prosopis* sp.) and spiny bromeliads (*Bromelia* sp.).

Wetzel and Lovett (1974) reported seven specimens of *Pseudoryzomys simplex* from similar habitats 280 km to the northwest in the central Chaco, near Juan de Zalazar. All of their animals were trapped in grass, on the floodplain of the Río Verde or in openings surrounded by thorn forest.

Habitat information is available for only two other specimens, trapped in Departamento Beni, eastern Bolivia. Both collection localities are generally characterized by a mosaic distribution of lowland tropical forests and seasonally flooded savannas. One specimen was taken on the ground in a grassland known locally as the Pampa de Meio on the left bank of the Río Iténez a few kilometers upstream from the Brazilian town of Costa Marques. No explicit information about trap placement accompanies the second specimen, collected near the Estación Biológica del Beni.

Ecological data are lacking from other specimens of *Pseudoryzomys simplex,* all of which, however, were collected in regions where unforested lowland habitats predominate: the Chaco Boreal (one specimen from Departamento Santa Cruz, Bolivia; another from Provincia Formosa, Argentina), the Caatinga (west of Recife in Estado Pernambuco, Brazil), and the Cerrado (Lagoa Santa).

The available evidence, while not over-

Fig. 4. Seasonally flooded *pantanal* habitat in the central Chaco 295 km (by road) NW Villa Hayes, Departamento Presidente Hayes, Paraguay. *Pseudoryzomys simplex* was collected in similar habitats near Villa Hayes. The photograph was taken only a few kilometers from Juan de Zalazar, where Wetzel and Lovett (1974) collected seven specimens of *P. simplex*.

whelming in detail, is at least consistent in suggesting that *Pseudoryzomys simplex* is a creature of open (unforested) tropical and subtropical lowland habitats. Of 11 specimens for which explicit trapping data are available, all were taken on the ground in grassy situations. None was actually caught in marshes, although seasonal flooding appears typical of some recorded capture localities.

MISIDENTIFICATIONS: Following Moojen (1952) and Avila-Pires (1960), the specific epithet *simplex* is often combined with the genus-group name *Oecomys* in reference to a muroid species said to inhabit the Cerrado of central Brazil (see Alho, 1982, and Mares et al., 1989, for references). Moojen (1952), however, provided no distinguishing characters nor any justification for this taxonomic combination, whereas Avila-Pires (1960) illustrated the skull and listed measurements of a specimen that is clearly not *Pseudoryzomys simplex*. Pending appropriate museum determinations based on voucher specimens, the identity of the animal known as "*Oecomys simplex* (Winge)" in the Brazilian ecological literature will remain uncertain.

SPECIMENS EXAMINED: ARGENTINA, Provincia Formosa, Tacaagle on Río Porteño (FMNH 34236). BOLIVIA, Departamento Beni, Estación Biológica del Beni (AMNH 262048), Pampa de Meio on Río Iténez (AMNH 210054), San Joaquín (FMNH 118810, USNM 364749); Departamento Santa Cruz, Velasco Santa Ana (USNM 390668). BRAZIL, Estado Minas Gerais, near Lagoa Santa (the lectotype and 24 paralectotypes in the Universitets Zoologisk Museum, Copenhagen); Estado Pernambuco, 40 km W Recife (UMMZ 164995–164998).

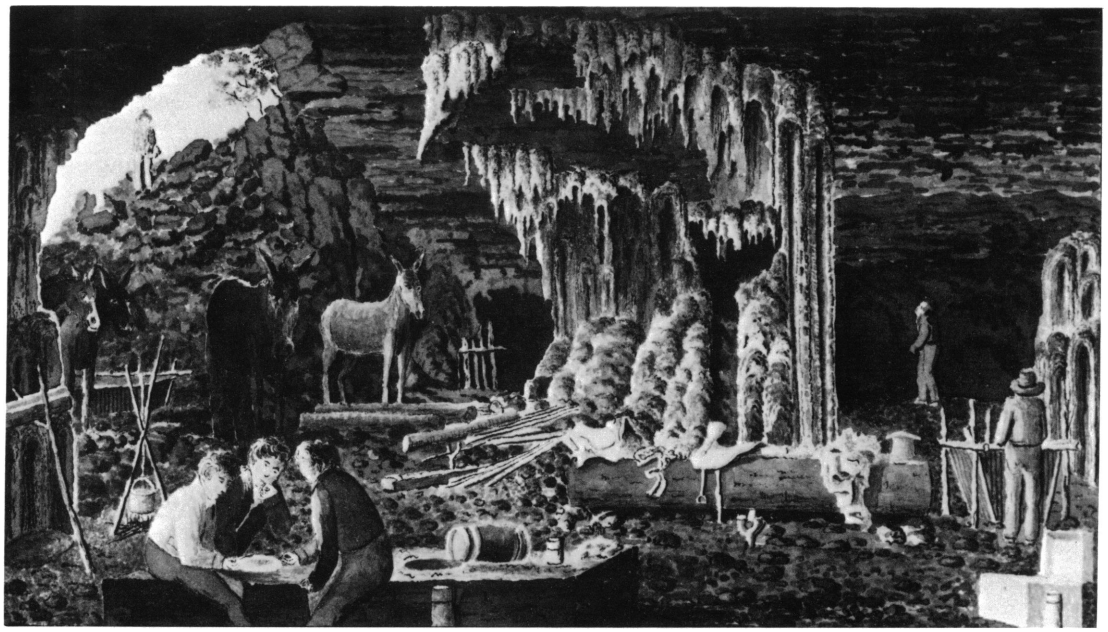

Fig. 5. The excavation of a cave (*Lapa do Mosquito*) near Lagoa Santa, Minas Gerais, Brazil. From an inkwash sketch by Peter Andreas Brandt, Lund's illustrator. Reproduced by permission from Brandt's original in the Universitets Zoologisk Museum, Copenhagen.

PARAGUAY, Departamento Presidente Hayes, Jesamatathla (BMNH 20.12.18.16, the type of *wavrini*), near Juan de Zalazar (CONN 15678, 15741, 15757, 15910, 16487, 16488, 17060), Misión (BMNH 20.12.18.15), 24 km NW Villa Hayes (UMMZ 133912, 133913, 134387). TOTAL: 47.

THE LAGOA SANTA CAVE FAUNAS

The 151 species of mammals reported by Winge from the Lagoa Santa cave deposits represent over 100 genera in 39 families and 12 orders (table 3). Between 10 and 20 percent of the species are extinct, but the certainty with which extinctions can be identified varies considerably from taxon to taxon. Five species of ground sloths, two glyptodonts, one canid (*Protocyon*), two bears (*Arctodus*), one saber-toothed cat, one litoptern, one notoungulate, one gomphothere, three horses, and one camel (*Paleolama*) have been unambiguously extinguished from the South American fauna since their preservation in cave sediments. Apparent extinctions among taxa of smaller, less conspicuous mammals, however, are more difficult to evaluate.

Some species that Winge reported from cave deposits are not represented among the Recent specimens that Lund and his colleagues trapped or shot around Lagoa Santa, but are definitely known to be extant elsewhere. The didelphid marsupial *Lutreolina crassicaudata* is an example, as is the echimyid rodent *Kannabateomys amblyonyx*. The absence of such species from Lund's Recent collections may either reflect extinctions of local populations or the difficulty of trapping or shooting animals whose behavior renders them less accessible to human observation. For *Lutreolina* and *Kannabateomys*, at least, taxonomic determinations are straightforward and continental extinctions are clearly not involved.

The case of *Pseudoryzomys simplex*, however, illustrates a commoner and much more difficult impediment to faunal interpretation for groups whose systematics remain poorly understood. Despite Winge's explicit statement that *Hesperomys simplex* was found in Recent owl pellets as well as in cave soils, the species has been regarded as a Pleistocene taxon or of dubious taxonomic affinities, its identity with *Pseudoryzomys wavrini* long

TABLE 3

Taxonomic Composition of the Lagoa Santa Cave Faunas and a Preliminary Assessment[a] of Quaternary Extinctions

Taxon[b]	Species in cave faunas	Extinct	
		Number	Percent
Marsupialia			
Didelphidae	12	0	0
Chiroptera			
Emballonuridae	1	0	0
Phyllostomidae	14	0	0
Natalidae	1	0	0
Vespertilionidae	6	1?	17
Molossidae	5	0	0
Primates			
Callitrichidae	1	0	0
Cebidae	4	1?	25
Hominidae	1	0	0
Edentata			
Megalonychidae	1	1	100
Megatheriidae	1	1	100
Mylodontidae	3	3	100
Dasypodidae	8	3	38
Glyptodontidae	2	2	100
Myrmecophagidae	2	0	0
Lagomorpha			
Leporidae	1	0	0
Rodentia			
Sciuridae	1	0	0
Muridae	25	7?	28
Erethizontidae	3	1	33
Caviidae	4	3	75
Hydrochaeridae	2[c]	1	50
Agoutidae	3[d]	2	67
Dasyproctidae	1	0	0
Myocastoridae	1	0	0
Octodontidae	1	1	100
Echimyidae	8	1	13
Carnivora			
Canidae	7	3?	43
Ursidae	2	2	100
Procyonidae	2	1	50
Mustelidae	5	0	0
Felidae	7	1	14
Litopterna			
Macraucheniidae	1	1	100
Notoungulata			
Toxodontidae	1	1	100
Proboscidea			
Gomphotheriidae	1	1	100
Perissodactyla			
Equidae	3	3	100
Tapiridae	2	1	50
Artiodactyla			
Tayassuidae	3	1?	33
Camelidae	1	1	100
Cervidae	4	0	0

[a] See text for explanation. Data compiled from Winge (1887, 1893a, 1893b, 1895–96a, 1895–96b, 1906, 1915).

[b] Familial classification of extinct taxa follows Marshall et al. (1984).

[c] "*Hydrochoerus capivara*" varieties "*typica*" and "*giganteus*" counted as separate species.

[d] "*Coelogenys paca*" varieties "*typica,*" "*laticeps,*" and "*major*" counted as separate species.

unsuspected. Seven muroid species described by Winge from the Lagoa Santa caves are currently unreported from Recent faunas (table 4), but determining whether these represent real extinctions or just other cases of unrecognized synonymies similar to that reported here for *P. simplex* will require careful reexamination of the type material and relevant comparisons with specimens of extant taxa. Massoia (1980), for example, pointed out the similarity of Winge's *Hesperomys molitor* (known only from cave deposits) to *Holochilus magnus,* a species named by Hershkovitz in 1955 from Recent Uruguayan material; future comparisons of these two taxa may show that they too are actually conspecific. Avila-Pires (1960) suggested that Winge's *Calomys plebejus* (another candidate for extinct status) is a living member of the genus *Delomys,* but this hypothesis has yet to be confirmed by direct comparisons of Recent material with the fossil type; similar uncertainties concern identifications proposed in the same paper for Winge's *Calomys rex* and *Habrothrix orycter.* No Recent specimens resembling Winge's *Habrothrix clivigensis* and *H. angustidens* are known from new collections made by Brazilian researchers near Lagoa Santa, and it has been suggested that both species are extinct (Avila-Pires, 1960). Winge's *Oxymycterus cosmodus, Cal-*

TABLE 4
The Muroid Rodent Fauna of the Lagoa Santa Caves (after Winge, 1887), an Updated Taxonomy, and Records of Recent Occurrence

Original name	Current taxonomy	Recent occurrence
Hesperomys simplex	*Pseudoryzomys simplex*[a]	yes[b]
H. molitor	*Holochilus molitor*[a]	unrecorded
H. tener	*Calomys laucha*[c]	yes[d]
H. expulsus	*C. callosus*[c]	yes[d]
Sigmodon vulpinus	*Holochilus brasiliensis*[e]	yes[d]
Habrothrix cursor	*Akodon cursor*[f]	yes[d]
H. clivigensis	*A. clivigensis*[f]	unrecorded
H. orycter	*A. nigrita*[g]	yes[d]
H. angustidens	*A. angustidens*[f]	unrecorded
H. lasiurus	*Bolomys lasiurus*[h]	yes[d]
Oxymycterus breviceps	*Blarinomys breviceps*[i]	yes[i]
O. talpinus	*Juscelinomys talpinus*[j]	unrecorded
O. rufus	*Oxymycterus roberti*[g]	yes[d]
O. cosmodus	*O. cosmodus*	unrecorded
Scapteromys labiosus	*Bibimys labiosus*[a]	yes[d]
S. principalis	*Kunsia tomentosus*[k]	yes[d]
S. fronto	*K. fronto*[k]	yes[l]
Calomys anoblepas	*Oryzomys anoblepas*[f]	unrecorded
C. longicaudatus	*Oligoryzomys eliurus*[m]	yes[d]
C. plebejus	*Delomys plebejus*[g]	yes[g]
C. rex	*Oryzomys ratticeps*[g]	yes[g]
C. coronatus	*O. coronatus*[f]	unrecorded
C. laticeps	*O. subflavus*[g]	yes[d]
Rhipidomys mastacalis	*Rhipidomys masatacalis*	yes[d]
Nectomys squamipes	*Nectomys squamipes*	yes[d]

[a] Massoia (1980).
[b] Winge (1887) and this report.
[c] Hershkovitz (1962).
[d] Winge (1887).
[e] Hershkovitz (1955).
[f] Trouessart (1898).
[g] Avila-Pires (1960).
[h] Reig (1978).
[i] Thomas (1896).
[j] Moojen (1965).
[k] Hershkovitz (1966).
[l] Hershkovitz (1966) referred Recent specimens to *K. f. chacoensis,* restricting *K. f. fronto* to the Lagoa Santa cave material.
[m] Brazilian populations of the *longicaudatus* group of *Oligoryzomys* are now referred to *eliurus,* but recent reviewers differ concerning the status of the latter (Myers and Carleton, 1981; Carleton and Musser, 1989).

omys anoblepas, and *C. coronatus* have received, to the best of our knowledge, no mention at all in the literature of systematic mammalogy since Trouessart (1898), and no conclusions regarding their true taxonomic affinities or their possible survival to Recent times are possible without critical reexamination of the type material.

Muroids are just one component of the Lagoa Santa cave faunas but, with 25 species recorded, they are unquestionably the best-sampled mammalian family-group taxon represented. Our experience with muroid specimens in the Lund collections convinces us that Winge had a remarkably discriminating eye for mammalian variation. We do not doubt that most (or all) of the taxa he identified represent distinct biological species. By contrast with the meager fragments—single molars or isolated mandibles—on which many fossil muroid taxa are based, muroids in the Lagoa Santa cave faunas are represented by excellent material, usually partial skulls with intact rostra, palates, and entire maxillary dentitions. Winge's competent sorting documented a muroid fauna of unparalleled diversity in the South American fossil record, and the quality of his specimens provides an unusual opportunity for confident systematic and biogeographic inference

TABLE 5
Occurrence of Muroid Rodent Species and Extinct Megafauna in Caves Excavated by Lund Near Lagoa Santa
(Table entries are numbers of species)

Cave	Muroid[a]	Ground sloths[b]	Glypto-donts[b]	Bears[c]	Saber-tooths[c]	Noto-ungu-lates[d]	Gompho-theres[d]	Equids[d]	Camels[d]
Capao Seco	10	1							
Cerca Grande	1	1							
Escrivania 3	3								
Escrivania 5	16	4	1	1	1	1	1	1	1
Escrivania 11	4	1	1				1	1	1
Lagoa do Semidouro	2	2		1				1	1
Marinho 2	2	1							
Quebra Chavelha	1								
Serra das Abelhas	15	1							
Tatus	1	2							

[a] From Winge (1887).
[b] From Winge (1915).
[c] From Winge (1895–96b).
[d] From Winge (1906).

as these collections are restudied. The results of future revisionary systematic efforts should facilitate the identification of real extinctions (if any) among muroids and other problematic taxa in the Lagoa Santa cave faunas, although the absence of stratigraphic control will remain a serious hindrance to historical interpretation.

Winge carefully distinguished skeletal material of small mammals recovered in Recent owl pellets from that excavated from cave sediments, but there is no other stratigraphic information accompanying any specimens from Lagoa Santa. Only ^{14}C dating of the bones themselves might offer a basis for chronological sorting, but the prospect is unpromising (see Taylor, 1980, 1987). Such historical conclusions as may emerge from reanalyses of the Lagoa Santa cave faunas must therefore be based, insofar as possible, on the indirect evidence of gross association.

Muroids were recovered from 10 caves (or cave chambers), of which 8 also yielded remains of the extinct megafauna (table 5). *Lapa da Escrivania Nr. 5* is noteworthy for having the largest muroid inventory as well as a virtually complete roster of the giant edentates, bears, saber-toothed cats, gomphotheres, and archaic ungulates known from Lagoa Santa. Although there is no evidence to prove the simultaneity of muroid and megafaunal deposition, neither is there reason to doubt that many muroid taxa were contemporaneous with the extinct large mammals found in the same caves. Nevertheless, because muroids presumably accumulated in cave soils for millennia after the megafaunal extinctions occurred, the historical intervals sampled by muroid and megafaunal remains are not comparable. Quantitative comparisons of extinctions among muroids (or didelphid marsupials, or bats) and larger mammals in the Lagoa Santa faunas (e.g., as provided in the last column of table 3) should therefore be interpreted with caution.

Abundant records of late Quaternary extinctions preclude assumptions of evolutionary equilibrium in ecological discussions of present-day faunas of large mammals on most continents (Martin, 1984) and of smaller vertebrates on many oceanic islands (Cassels, 1984; Olson and James, 1984). It is possible, however, that such assumptions are not inappropriate for some continental faunas of small mammals. Voss (1988), for example, speculated that the living muroid rodents of South America represent a substantially intact adaptive radiation, and similar claims might plausibly be made for South American phyllostomid bats and murine oppossums. If

the presence of many extinct species of these groups in the Lagoa Santa cave collections were to be established by revisionary systematic studies, such conjectures would be seriously compromised. Perhaps, as for large mammals, extant faunas of Neotropical small mammals are but pale shadows of their late Pleistocene diversity. Reanalyses of the Lagoa Santa fossils therefore promise an opportunity to evaluate ecological inferences concerning Recent mammalian communities.

Revised taxonomic determinations for Lagoa Santa muroids will also provide materials to judge the plausibility of biogeographic hypotheses about historical centers of origin. Reig (1984), for example, identified regions of maximum diversity for various suprageneric groups of Neotropical muroids and proposed that these correspond to "areas of original differentiation." Leaving aside the questionable phylogenetic integrity of most suprageneric groups of South American muroids (see Voss, 1988, and Carleton and Musser, 1989, for caveats), the practice of inferring areas of historical origin from areas of contemporary diversity minimally requires that the biotic landscape has remained geographically stable within the relevant geologic time frame. Quaternary faunas whose phylogenetic composition is grossly unlike modern ecological communities in the same general region would undermine the credibility of such hypotheses. Few Quaternary faunas of Neotropical small mammals have been reported, but Pearson (1987) and Tonni et al. (1988) documented late Pleistocene or early Holocene muroid assemblages from temperate South America that are similar to present-day communities in the same areas. The much larger, tropical fauna from Lagoa Santa, when revised, will contribute to the active debate concerning the evolutionary geography of South American muroids.

Finally, to reiterate a point made earlier in another context, and with the example of *Pseudoryzomys simplex* again in mind, it seems probable that additional taxa described by Winge from Lagoa Santa cave material are unrecognized synonyms of species currently known by different names. Although this, as a purely nomenclatural issue, is the least biologically compelling motivation for renewed studies of Lund's collections, the object of taxonomic research is ultimately to facilitate the transfer of information among researchers, whether their primary focus is Pleistocene or Recent organisms. Identifying redundancies in the Linnaean system contributes to the accuracy and effectiveness of such communication.

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